UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

LA RELATION DIVERSITÉ-STABILITÉ DANS LES ÉCOSYSTÈMES FORESTIERS : MÉCANISMES ET IMPLICATIONS FACE AUX CHANGEMENTS CLIMATIQUES

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RAPHAËL AUSSENAC

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AVANT-PROPOS

Ce mémoire de thèse ainsi que les articles qu'il contient présentent les contributions scientifiques originales de mon doctorat en Science de l'Environnement, réalisé à l'Université du Québec en Abitibi-Témiscamingue (UQAT) de 2014 à 2017.

Ce travail de recherche s'articule en cinq parties : une introduction générale, trois chapitres et une conclusion générale. Chaque chapitre correspond à un article scientifique qui a été ou sera publié dans une revue à comité de lecture. De ce fait, chaque chapitre peut être lu indépendamment. Les chapitres 1 à 3 correspondent aux articles suivants :

1. Raphaël Aussenac, Yves Bergeron, Claudele Ghotsa Mekontchou, Dominique Gravel, Kamil Pilch, Igor Drobyshev. (2017). "Intraspecific variability in growth response to environmental fluctuations modulates the stabilizing effect of species diversity on forest growth". *Journal of Ecology*.
2. Raphaël Aussenac, Yves Bergeron, Dominique Gravel, Igor Drobyshev. "Interactions among trees: a key element in the stabilizing effect of species diversity on forest growth".
3. Raphaël Aussenac, Yves Bergeron, Loïc D'Orangeville, Louis Duchesne, Dominique Gravel, Daniel Houle, Igor Drobyshev. "The stabilizing effect of species diversity on forest productivity under climate change".

Les paragraphes qui suivent précisent le rôle des co-auteurs dans la réalisation de chacun des chapitres.

Dans le chapitre 1, R.A., Y.B., D.G. et I.D. ont défini les objectifs et conçu la méthodologie. R.A. et K.P. ont collecté les données sur les dispositifs expérimentaux de la FERLD (Forêt d'Enseignement et de Recherche du Lac Duparquet) et 3 placettes expérimentales gérées par le laboratoire d'écologie intégrative de l'Université de Sherbrooke. R.A., C.G.M. and K.P. ont analysé les données. Enfin R.A a dirigé l'écriture du manuscrit.

Dans le chapitre 2, R.A., Y.B., D.G. et I.D. ont défini les objectifs et conçu la méthodologie. Les données sont celles qui ont servi dans le chapitre 1. R.A. a analysé les données et dirigé l'écriture du manuscrit.

Enfin, dans le chapitre 3, R.A., Y.B., L.D'O., L.D., D.G., D.H. et I.D. ont défini les objectifs et conçu la méthodologie. Les données proviennent de l'inventaire forestier du Québec. R.A. et L.D'O. ont analysé les données. Enfin R.A a dirigé l'écriture du manuscrit.

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RÉSUMÉ

Un nombre croissant d'études suggère que la diversité stabilise la productivité des écosystèmes. L'effet stabilisant de la diversité reposerait principalement sur l'asynchronicité de réponse des espèces aux fluctuations environnementales et sur les interactions entre espèces. Ces deux mécanismes découlent de la complémentarité des espèces ; deux espèces étant d'autant plus complémentaires que leurs niches écologiques sont différentes. Les interactions entre espèces pourraient également jouer un rôle central dans la relation diversité-stabilité en contrôlant les dynamiques de populations. Toutefois, les mécanismes qui gouvernent l'effet stabilisant de la diversité sont encore mal compris.

Les forêts offrent un certain nombre d'avantages pour étudier les mécanismes qui sous-tendent la relation diversité-stabilité. En effet, dans les écosystèmes forestiers, l'effet stabilisant de la complémentarité des espèces peut être étudié sans effets confondants dus aux dynamiques de populations. Cela tient à la durée de vie élevée des arbres qui implique des dynamiques de populations lentes. Sur des périodes courtes, relativement à l'espérance de vie des arbres, la relation diversité-stabilité peut donc être étudiée dans des communautés où les populations restent constantes. Dans ce cas, l'effet stabilisant de la diversité reposerait principalement sur la complémentarité des espèces et non sur des mécanismes liés aux dynamiques de populations. Comprendre la relation diversité-stabilité dans les écosystèmes forestiers est également essentiel étant donné l'importance de ces écosystèmes pour l'humanité et leur vulnérabilité aux changements globaux.

Cette thèse a pour objectifs (i) de tester si la diversité stabilise la productivité des forêts tempérées et boréales de l'Est du Canada, (ii) d'identifier les mécanismes qui gouvernent cette relation diversité-stabilité, et (iii) de déterminer si la richesse spécifique peut stabiliser la croissance des forêts face aux changements climatiques. La relation diversité-stabilité a été étudiée dans des communautés où les populations étaient maintenues constantes, notamment en travaillant sur de courtes périodes, relativement à l'espérance de vie des arbres. Ainsi, nous avons pu étudier le rôle de la complémentarité des espèces dans l'effet stabilisant de la diversité indépendamment des mécanismes liés aux dynamiques de populations.

Les trois chapitres de cette thèse mettent en évidence un effet stabilisant de la diversité sur la croissance des forêts. Cet effet est dû, notamment, à l'asynchronicité de croissance des individus hétérospécifiques. Cette asynchronicité de croissance des individus provient de leur différence de réponses aux fluctuations climatiques et de leur sensibilité différentielle aux insectes phytophages. La diversité stabilise également la croissance des forêts en induisant des interactions favorables entre les individus. Ces interactions favorables peuvent augmenter la croissance individuelle et tamponner la réponse des arbres aux fluctuations climatiques. Cet effet stabilisant de la diversité pourrait se maintenir face aux changements climatiques.

A la lumière de ces résultats, augmenter la diversité des peuplements apparaît comme une stratégie permettant de stabiliser les revenus de l'exploitation forestière, notamment face aux changements climatiques. Afin de maximiser l'effet stabilisant de la diversité les mélanges d'espèces ayant des niches écologiques complémentaires pourraient être favorisés. Nos résultats rejoignent ainsi un nombre grandissant d'études appelant à augmenter la diversité dans les peuplements forestiers.

Cette thèse met en évidence l'effet stabilisant de la diversité dans les écosystèmes forestiers et permet de mieux comprendre les mécanismes qui sous-tendent la relation diversité-stabilité. Toutefois un certain nombre d'incertitudes demeurent. Des études supplémentaires sont nécessaires afin de déterminer si l'effet stabilisant de la diversité sur la productivité forestière est généralisable à tous les types de forêts.

Mots-clés : diversité, stabilité, changements climatiques, croissance des arbres, fonctionnement des écosystèmes, forêts boréales, forêts tempérées

INTRODUCTION

Les activités humaines ont un impact considérable sur la biodiversité[1]. A l'échelle globale, elles entrainent une perte d'espèce. En effet, le taux d'extinction sur la période 1600-2016 serait 10 à 100 fois supérieur au taux historique, reconstitué à partir de fossiles (Vellend *et al.* 2017). Bien que ces estimations restent incertaines, notamment en raison d'un sous-échantillonnage de nombreux clades, elles semblent annoncer la sixième extinction de masse (Barnosky *et al.* 2011). Parmi les causes principales responsables de cette perte d'espèces on compte le changement d'utilisation des sols (i.e. la perte, la dégradation et la fragmentation des habitats des espèces; Krauss *et al.* 2010), les changements climatiques (Thomas *et al.* 2004), l'introduction d'espèces invasives (McGeoch *et al.* 2010) et la surexploitation des espèces (Rosser & Mainka 2002). A l'échelle locale, en revanche, les activités humaines ont des effets variables (Vellend *et al.* 2013). Si les espèces invasives et les changements climatiques tendent à diminuer la richesse spécifique, certaines interventions ou perturbations anthropiques peuvent augmenter le nombre d'espèces.

L'impact des activités humaines sur la biodiversité pourrait grandir à l'avenir. En effet, l'emprise territoriale de l'humanité ne cesse de s'étendre. Les terres cultivées et les

[1] La biodiversité peut se définir comme une mesure de la variété du vivant, qu'il s'agisse de gènes, d'espèces, ou de paysages. Dans ce document, toutefois, il s'agira essentiellement de la diversité des espèces, i.e. la richesse spécifique.

pâturages couvrent aujourd'hui environ 40% des terres émergées, souvent au détriment de la forêt, dont la surface a diminué de 7-11 millions de km^2 au cours des 300 dernières années (Foley *et al.* 2005). Parallèlement, les changements climatiques s'accélèrent. Les concentrations dans l'atmosphère de dioxyde de carbone (CO_2), de protoxyde d'azote (N_2O) et de méthane (CH_4), ont atteint des niveaux sans précédent depuis au moins 800 000 ans (Stocker, Dahe & Plattner 2013). De ce fait, chacune des trois dernières décennies a été successivement la plus chaude depuis 1850, et la période 1983-2012 est probablement la plus chaude depuis 800 ans dans l'hémisphère nord. On observe aussi une augmentation de la fréquence et de l'intensité des événements climatiques extrêmes. Par ailleurs, le commerce mondial et la mobilité croissante des populations humaines transportent un nombre toujours plus grand d'espèces potentiellement invasives ou pathogènes. Enfin, la surexploitation des espèces pourrait gagner en importance avec l'augmentation de la population humaine.

Changer la biodiversité pourrait considérablement affecter les écosystèmes. En effet, la biodiversité a un impact sur le fonctionnement des écosystèmes comparable, en magnitude, à celui du climat ou de la concentration en CO_2 (Cardinale *et al.* 2012; Hooper *et al.* 2012). Une réduction de la biodiversité est généralement associée à une moindre efficacité des fonctions écosystémiques[2] et à une diminution de leur stabilité temporelle. De ces fonctions dépendent des services écosystémiques[3] essentiels au bien-être de l'humanité. Or, les sociétés humaines dépendent directement de la prévisibilité, et donc de la stabilité temporelle, de ces services. Comprendre les mécanismes qui sous-tendent la relation diversité-stabilité est donc crucial.

[2] Processus contrôlant les flux d'énergies, de nutriments et de matières organiques dans un écosystème, e.g. capture de ressources, production de biomasse, décomposition, recyclage des éléments nutritifs. La production de biomasse correspond, par exemple, au processus par lequel les plantes utilisent la lumière pour convertir des matières inorganiques en tissus biologiques (Cardinale *et al.* 2012).

[3] Bénéfices que les écosystèmes fournissent à l'humanité, e.g. régulation du climat, filtration de l'eau, production d'aliment, de bois, de fibre (Cardinale *et al.* 2012).

0.1 Perspectives historiques

L'idée que la stabilité est positivement corrélée à la biodiversité apparaît dans les années 1950. Elle reposait alors sur des raisonnements intuitifs et des observations qualitatives. Initialement, Odum (1953) s'est intéressé à la relation entre la redondance dans les chaines trophiques et la stabilité des flux d'énergies passant à travers elles. La redondance peut ici s'interpréter comme une mesure du nombre de prédateurs ou de proies associé à chaque espèce, et donc comme une mesure de diversité. Selon Odum, l'augmentation de la redondance, augmente la stabilité du débit énergétique dans les chaines trophiques. Les communautés les plus stables étant celles pour lesquelles on observe le moins de changement dans le flux d'énergie avec l'élimination aléatoire d'une espèce. Plus tard, MacArthur (1955) arrive à des conclusions similaires. Il définit la stabilité comme une mesure de la réponse des communautés à une perturbation qui influence la densité d'au moins une espèce. Il démontrera qu'un plus grand nombre d'interactions trophiques stabilise les communautés, car cela diminue l'interdépendance des densités de populations et donc limite la propagation des perturbations. Enfin, les observations de Elton (1958) viennent, elles-aussi, étayer l'hypothèse d'une relation positive entre diversité et stabilité. Il observe, par exemple, que les densités de populations fluctuent violemment dans les forêts boréales, pauvres en espèces, notamment à cause des épidémies d'insectes phytophages. Comparativement, les densités de populations sont plus stables dans les forêts tropicales, riches en espèces, où de telles épidémies ne se produisent pas. Il en conclura que la diversité des prédateurs et des parasites dans les communautés riches en espèces empêche l'expansion brutale des populations (dont les populations d'insectes phytophages) et ainsi stabilise les communautés. A la fin des années 1960, la corrélation positive entre diversité et stabilité est unanimement acceptée, malgré un manque de fondations théoriques et expérimentales.

Dans les années 1970, le consensus autour de l'effet stabilisant de la diversité est largement remis en question. Le travail le plus influent de cet époque est celui de May (1973). Ce dernier observait que la diversité tendait à déstabiliser les communautés. Il montrait plus précisément que la probabilité qu'une communauté construite aléatoirement soit stable décroit avec le nombre d'espèce et la connectance entre les espèces ; la connectance correspond ici à la probabilité que les espèces interagissent. May définissait la stabilité comme étant la probabilité que la taille de la population de chaque espèce dans une communauté revienne à l'équilibre suite à une perturbation dans la taille de la population d'une des espèces. L'explication intuitive à cet effet déstabilisant était qu'un plus grand nombre d'espèces et de connections permettait aux perturbations de se propager davantage dans les communautés. Ces résultats vont répandre l'hypothèse selon laquelle la diversité a un rôle déstabilisant dans les communautés, contrairement à ce que proposaient initialement Odum, MacArthur et Elton. Pimm (1984) explique cette divergence de résultats par la multitude de définitions associées aux concepts de diversité et de stabilité (Tableau 0.1). Il souligne également que ces concepts sont appliqués à différentes variables d'intérêt (e.g. abondances des populations, composition en espèces des communautés), permettant d'obtenir une grande variété de relations diversité-stabilité.

Dans les années 1990 et 2000, l'hypothèse d'une relation positive entre diversité et stabilité est de nouveau proposée. Une avancée majeure de cette époque réside dans la distinction des niveaux d'organisation écologique dans lesquels la diversité et la stabilité sont mesurées. La distinction entre stabilité des populations et stabilité des communautés apparait. De même, émerge la distinction entre diversité verticale (e.g. richesse spécifique d'un réseau trophique) et diversité horizontale (e.g. richesse spécifique d'un unique niveau trophique). Ces nouvelles perspectives vont conduire à l'étude du lien entre diversité et stabilité des fonctions écosystémiques, jetant les bases de la nomenclature contemporaine des recherches portant sur la relation diversité-stabilité. Ces dernières s'intègrent aujourd'hui dans un champ de recherche plus large

appelé *BEF* (*Biodiversity Ecosystem Functioning*), qui s'intéresse aux multiples effets de la diversité sur le fonctionnement des écosystèmes.

La *stabilité temporelle* (ST; Tilman 1999) va s'imposer comme mesure de la stabilité dans de nombreuses études. Cette dernière correspond à l'inverse du coefficient de variation et se calcule donc comme suit :

$$ST = \frac{\mu}{\sigma} \qquad \text{(eqn 0.1)}$$

où μ et σ sont, respectivement, la moyenne et la variance d'une fonction écosystémique (e.g. la production annuelle de biomasse d'un écosystème). Cette mesure de la stabilité a l'avantage d'être facile à mesurer et d'intégrer les effets combinés de la résistance et de la résilience (Tableau 0.1). Par ailleurs, la variance étant standardisée par la moyenne, cette mesure permet de prendre en compte la tendance de la variabilité à augmenter avec la moyenne, ce qui permet de comparer les niveaux de stabilité entre différents types d'écosystèmes.

Tab. 0.1: Concepts et définitions reliés à la diversité et à la stabilité dans les systèmes écologiques (modifié de Pimm 1984; Loreau 2010)

Diversité (ou complexité)	
Richesse spécifique	Le nombre d'espèces dans un système.
Connectance	Le nombre d'interactions interspécifiques divisé par le nombre possible d'interactions interspécifiques.
Force des interactions	L'amplitude moyenne des interactions interspécifiques : la force de l'effet de la densité d'une espèce sur le taux de croissance d'une autre.
Équitabilité des espèces	La variance de l'abondance des espèces (mesurée par exemple par l'indice de diversité de Shannon : *H*).
Stabilité	*Définition*
Stabilité qualitative	Propriété d'un système qui retourne à son état initial après une perturbation.
Résilience	Une mesure de la vitesse à laquelle un système retourne à son état initial après une perturbation.
Résistance	Une mesure de la capacité d'un système à maintenir son état initial face à une perturbation.
Robustesse	Une mesure de la quantité de perturbation qu'un système tolère avant de changer d'état.
Amplification d'enveloppe	Décrit comment une perturbation est amplifiée dans un système à l'équilibre.
Variabilité	Une mesure de la magnitude des changements temporels dans une propriété d'un système.
Persistance	La mesure de la capacité d'un système à se maintenir dans le temps.
Variable d'intérêt	
Abondance de chaque espèces	La densité de toutes les espèces dans le système.
Composition en espèce	La liste de toutes les espèces dans le système.
L'abondance d'un niveau trophique	La densité totale (ou biomasse) de toutes les espèces dans un niveau trophique.
Propriété d'un écosystème	Par exemple la productivité.

0.2 Bases théoriques de la relation diversité-stabilité

Les bases théoriques d'une relation positive entre diversité et stabilité des fonctions écosystémiques reposent principalement sur la notion de complémentarité des espèces. Cette complémentarité correspond aux différences de niches écologiques[4] entre les espèces ; deux espèces étant d'autant plus complémentaires que leurs niches écologiques sont différentes. Pour plus de simplicité, la production annuelle de biomasse (ou productivité) sera prise comme exemple de fonction écosystémique par la suite. Selon *l'hypothèse d'assurance*, la richesse spécifique augmente la stabilité de la productivité des communautés par le biais de la complémentarité des espèces (Yachi & Loreau 1999). Cette hypothèse repose sur un principe simple : du fait des différences de niches écologiques, chaque espèce a une réponse aux fluctuations environnementales qui lui est propre. Face à des fluctuations environnementales, différentes espèces ont donc des réponses plus ou moins asynchrones. Ainsi, dans des communautés riches en espèces, des compensations de productivité entre espèces peuvent apparaître. Ces compensations peuvent augmenter la stabilité (*ST*) de la productivité à l'échelle de la communauté, en diminuant sa variance (σ). On peut donc s'attendre à ce que la stabilité de la productivité des communautés augmente avec le nombre d'espèces et l'asynchronicité de leurs réponses. C'est ce qu'on appelle *l'effet portfolio* (Doak *et al.* 1998; Tilman, Lehman & Bristow 1998). Toutefois, de Mazancourt *et al.* (2013) ont démontré analytiquement que l'effet stabilisant de l'asynchronicité de réponse des espèces aux fluctuations environnementales diminue avec la variabilité intraspécifique des réponses. En effet, si cette variabilité est élevée, on peut s'attendre à ce que des individus appartenant à des espèces dont les réponses moyennes sont asynchrones aient des réponses similaires (i.e. synchrones). L'effet stabilisant de l'asynchronicité de réponse des espèces s'en trouverait ainsi limité. La

[4] Ensemble des conditions environnementales permettant aux espèces de former des populations viables.

richesse spécifique pourrait également augmenter la productivité des communautés (μ) par le biais de la complémentarité des espèces, et ainsi stabiliser d'avantage les communautés (i.e. augmenter *ST*). En effet, chaque espèce ayant des besoins différents, une communauté riche en espèce pourrait exploiter plus complètement son environnement qu'une communauté pauvre en espèces et ainsi être plus productive. Par ailleurs, selon la théorie de la coexistence (Chesson 2000), la compétition[5] interspécifique tend à être moins forte que la compétition intraspécifique en raison des différences de niches écologiques entre les espèces. De plus, de la facilitation[6] peut apparaitre entre les espèces. En réduisant la compétition et en augmentant la facilitation entre les espèces, la diversité pourrait, là encore, augmenter la productivité des communautés.

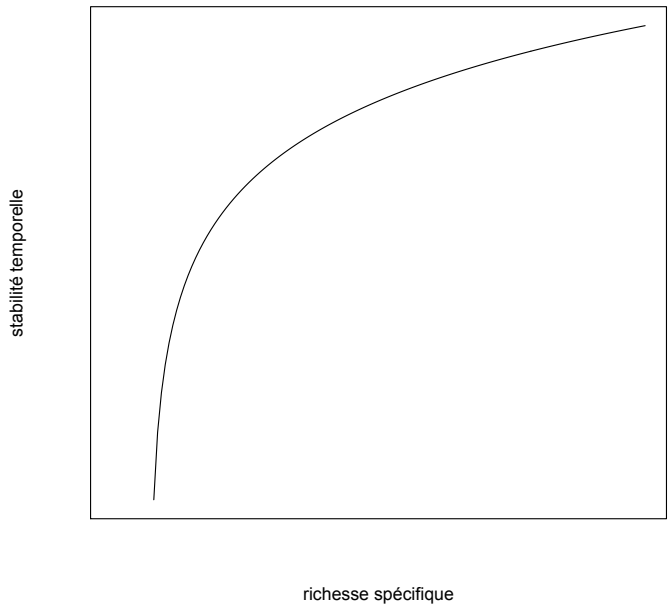

Fig. 0.1 : Saturation de la relation diversité-stabilité due à la redondance fonctionnelle des espèces.

[5] Effet négatif du partage des ressources sur la croissance des espèces.
[6] Effet positif d'une espèce sur la croissance d'une autre.

La relation diversité-stabilité pourrait saturer en raison de la redondance fonctionnelle des espèces (Figure 0.1; Schulze & Mooney 1993). Cette dernière apparaît lorsque plusieurs espèces assurent les mêmes fonctions dans un écosystème. La redondance fonctionnelle pourrait donc augmenter avec la richesse spécifique. Ainsi, le potentiel stabilisant d'une augmentation de la richesse spécifique pourrait être plus faible dans les communautés riches en espèces que dans les communautés pauvres en espèces. De même, dans une communauté riche en espèces, une faible perte de diversité pourrait avoir un impact mineur sur la stabilité de la productivité. Dans ce cas, les fonctions des espèces disparues pourraient être assurées par les espèces restantes. En revanche, une perte plus importante de diversité pourrait affecter la stabilité de la productivité si aucune des espèces restantes ne peut assurer les fonctions précédemment assurées par les espèces disparues.

Les interactions entre espèces (i.e. compétition et facilitation) pourraient également jouer un rôle central dans la relation diversité-stabilité en contrôlant les dynamiques de populations. Différents mécanismes pourraient être à l'œuvre. Tout d'abord une augmentation de la richesse spécifique augmente la probabilité de rencontrer des espèces ayant un taux de croissance élevé, mieux adaptées aux conditions environnementales que les autres. L'avantage compétitif de ces espèces pourrait les amener à dominer, en abondance, les communautés. Ainsi la productivité des communautés pourrait être plus importante et donc plus stable, car une augmentation de μ augmente *ST*. Ce mécanisme est appelé *effet de sélection* (Loreau & Hector 2001). A mesure que les conditions environnementales changent (e.g. d'une année à l'autre), l'avantage compétitif pourrait passer d'une espèce à l'autre. Ainsi, quel que soit les conditions environnementales, les espèces les mieux adaptées (ayant les meilleurs taux de croissance) pourraient voir leur abondance augmenter au détriment des espèces moins performantes. La productivité des communautés pourrait donc être plus élevée et les compensations de productivité entre espèce plus complètes. En conséquence, la productivité des communautés pourrait être plus stable. Ces covariations négatives

d'abondances dues aux interactions entre espèces sont appelées *dynamiques compensatoires* (Gonzalez & Loreau 2009).

Les différents mécanismes théoriques présentés plus haut ont été décrit pour des communautés compétitives (i.e. ne comprenant qu'un seul niveau trophique). Dans les communautés multitrophiques (i.e. qui comprennent plusieurs niveaux trophiques), des mécanismes supplémentaires pourraient affecter la relation diversité-stabilité (Ives, Klug & Gross 2000; Thébault & Loreau 2005; Loreau 2010). Tout comme dans les communautés compétitives, la complémentarité et les interactions entre espèces sont à la base de ces mécanismes. Tout d'abord, l*'hypothèse d'assurance* (Yachi & Loreau 1999) pourrait s'appliquer dans les communautés multitrophiques. Dans ces dernières, les compensations de productivité pourraient se produire entre espèces appartenant à différents niveaux trophiques. La diversité pourrait également stabiliser la productivité des communautés multitrophiques en réduisant la force cumulée des interactions entre proies (ressources) et prédateurs (consommateurs). C'est par exemple le cas lorsque la diversité des proies oblige les prédateurs à consacrer plus de temps à distinguer les proies qu'ils consomment de celles qu'ils ne consomment pas, ce qui réduit leur consommation (Kratina, Vos & Anholt 2007). Les interactions proies-prédateurs ayant un effet déstabilisant, une réduction de leur force cumulée stabiliserait la productivité des communautés. Dans le cas où la diversité des proies augmenterait la force cumulée des interactions proies-prédateurs, une augmentation de la richesse spécifique déstabiliserait la productivité des communautés. Toutefois, ce dernier cas semble peu réaliste car il décrit des prédateurs généralistes pouvant consommer toujours plus de proies à mesures qu'elles entrent dans la communauté. C'est ce que décrivait implicitement May (1973) en affectant des coefficients d'interactions entre espèces indépendamment du nombre d'interactions trophiques.

0.3 Apports des études empiriques

De nombreuses études empiriques portant sur la relation diversité-stabilité ont été menées, essentiellement dans des communautés d'herbacées ou des microcosmes (Griffin *et al.* 2009; Jiang & Pu 2009; Hector *et al.* 2010; Cardinale *et al.* 2012). Le plus souvent, un effet stabilisant de la diversité sur la productivité des communautés a été observé. Conformément à la théorie, la complémentarité et les interactions entre espèces semblent jouer un rôle central dans l'effet stabilisant de la diversité. En effet, les diverses manifestations de la complémentarité ont été observées : (i) la diversité tend à augmenter la productivité des écosystèmes, (ii) cette augmentation tend à saturer à mesure que la diversité augmente, et (iii) différentes espèces ont tendance à répondre de manière asynchrone aux perturbations. Des *dynamiques compensatoires* ont également été rapportées (Allan *et al.* 2011; Mariotte *et al.* 2013). Un certain nombre d'études, toutefois, rapportent des résultats moins conformes aux prédictions théoriques. Le rôle de *l'effet de sélection* dans la relation diversité-stabilité reste, par exemple, à éclaircir. En effet, *l'effet de sélection* pourrait contribuer à l'effet stabilisant de la diversité dans certaines communautés de zooplanctons (Steiner 2005) ou dans des jeunes plantations d'arbres (Tobner *et al.* 2016), mais pas dans les communautés d'herbacées (Loreau & Hector 2001). D'autres études suggèrent l'existence de mécanismes additionnels gouvernant la relation diversité-stabilité. Zhang et Zhang (2006) observent, par exemple, que la diversité stabilise la productivité de communautés d'algues dans des milieux pauvres en nutriments. En revanche, cet effet stabilisant ne semble pas se produire dans des milieux enrichis en nutriments. Ainsi, l'effet stabilisant de la diversité pourrait dépendre de la richesse en nutriments des milieux. Enfin, certaines études rapportent une relation diversité-stabilité neutre ou négative. Gonzalez et Descamps-Julien (2004) observent, par exemple, qu'une augmentation de la richesse spécifique de communautés d'algues peut diminuer la stabilité temporelle de la productivité de biomasse à l'échelle de la communauté. En outre, si des progrès remarquables permettent aujourd'hui une meilleure

compréhension de la relation diversité-stabilité, des études supplémentaires sont indispensables pour tenter de concilier les prédictions théoriques et les résultats empiriques. Pour cela, l'identification des mécanismes qui gouvernent la relation diversité-stabilité dans différents types d'écosystèmes est primordiale.

0.4 Relation diversité-stabilité dans les écosystèmes forestiers

Les forêts offrent un certain nombre d'avantages pour étudier les mécanismes qui gouvernent la relation diversité-stabilité. Tout d'abord, la durée de vie élevée des arbres implique des dynamiques de populations plus lentes que dans d'autres écosystèmes (e.g. prairies, microcosmes). Sur des périodes courtes, relativement à l'espérance de vie des arbres (e.g. 20-30 ans), la relation diversité-stabilité peut donc être étudiée dans des communautés où les populations restent constantes. Dans ce cas, l'effet stabilisant de la diversité reposerait principalement sur la complémentarité des espèces et non sur des mécanismes liés aux dynamiques de populations (*effet de sélection* et *dynamiques compensatoires*). En d'autres termes, dans les écosystèmes forestiers, l'effet stabilisant de la complémentarité des espèces pourrait être étudié sans effets confondants dues aux dynamiques de populations. La durée de vie élevée des arbres permet également de travailler sur de longues séries temporelles de croissance, notamment grâce à l'utilisation de la dendrochronologie, ce qui permet d'obtenir des mesures fiables de l'asynchronicité de réponse des espèces aux fluctuations environnementales. Enfin, dans les écosystèmes forestiers, les individus (i.e. arbres) se distinguent facilement les uns des autres, ce qui n'est pas le cas dans d'autres types de communautés. Dans les communautés d'herbacées, par exemple, les individus sont souvent difficiles à définir en raison de la présence de parties semi-indépendantes. La distinction nette entre individus dans les écosystèmes forestiers pourrait permettre d'évaluer la variabilité intraspécifique de réponse aux fluctuations environnementales qui pourrait jouer un rôle dans l'effet stabilisant de la diversité (de Mazancourt *et al.* 2013).

Comprendre la relation diversité-stabilité dans les écosystèmes forestiers est également essentiel car ces derniers sont confrontés simultanément aux changements climatiques, potentiellement déstabilisants, et à une perte importante d'espèces. L'augmentation attendue des températures, par exemple, pourrait affecter la *ST* de la productivité des peuplements forestiers (Boisvenue & Running 2006; Bonan 2008; Lindner *et al.* 2010; Gauthier *et al.* 2015; Charney *et al.* 2016). Selon les espèces et les régions considérées, les températures plus chaudes pourraient augmenter ou réduire la productivité des peuplements (μ dans eqn 0.1) et, par conséquent, la *ST* de leur productivité. Par ailleurs, l'augmentation attendue de la fréquence et de l'intensité des événements climatiques extrêmes pourrait réduire la *ST* de la productivité des peuplements par le biais de trois mécanismes distincts. Tout d'abord, en augmentant la fréquence des anomalies de croissance et donc la variance de la productivité des peuplements (σ dans eqn 0.1; Latte, Lebourgeois & Claessens 2015; Ols *et al.* 2016). Ensuite, en augmentant la synchronicité de croissance des espèces, ce qui limite les compensations de croissance entre espèces et augmente, là encore, la variance de la productivité des peuplements (Latte, Lebourgeois & Claessens 2015; Shestakova *et al.* 2016). Enfin, en réduisant directement la productivité des peuplements (μ dans eqn 0.1; Lindner *et al.* 2014; Latte, Lebourgeois & Claessens 2015; Ols *et al.* 2016). Les changements climatiques pourraient également réduire la *ST* de la productivité des peuplements en augmentant la fréquence et l'intensité des perturbations comme les feux, les tempêtes ou les épidémies de pathogènes ou d'insectes phytophages (Dale *et al.* 2001; Seidl *et al.* 2017). Parallèlement, la foresterie moderne tend à réduire la richesse spécifique des forêts en favorisant les peuplements monospécifiques (Bremer & Farley 2010), ces derniers étant plus simple à gérer et à exploiter que des peuplements plus riches en espèces. L'absence de diversité de niches écologiques dans ces peuplements pourrait limiter leur capacité à se maintenir dans un environnement toujours plus variable. Ainsi, en réduisant la richesse spécifique des peuplements forestiers, la foresterie

moderne pourrait réduire la *ST* de leur productivité, notamment face aux changements climatiques.

A ce jour, très peu d'études se sont intéressées directement à l'effet de la diversité sur la stabilité temporelle de la productivité des peuplements forestiers. Conformément à la théorie et aux études empiriques menées dans d'autres écosystèmes, Jucker et al. (2014a) et Morin et al. (2014) montrent que la diversité stabilise la productivité des peuplements forestiers. Toutefois, ces deux études mettent en évidence des mécanismes différents pour expliquer cet effet stabilisant. Les différentes échelles de temps considérées pourraient expliquer ces divergences. En effet, Jucker et al. (2014a) ont utilisé des données dendrochronologiques pour reconstruire la productivité des peuplements sur une période de 20 ans. Leurs analyses n'intègrent donc pas les dynamiques de populations. Ils mettent en évidence trois mécanismes pour expliquer l'effet stabilisant de la diversité : (i) l'asynchronicité de réponse des espèces aux fluctuations environnementales, (ii) un effet positif de la diversité sur la productivité des peuplements, et (iii) un effet négatif de la diversité sur la variance de croissance des espèces. Ce dernier mécanisme suggère que les interactions favorables (i.e. compétition réduite et facilitation) entre individus hétérospécifiques tamponnent la réponse des espèces aux fluctuations environnementales. Morin et al. (2014), quant à eux, ont simulé l'évolution de peuplements forestiers sur 2000 ans à l'aide de modèles de succession intégrant les dynamiques des populations. Ils mettent en évidence deux mécanismes pour expliquer l'effet stabilisant de la diversité : (i) des *dynamiques compensatoires* entre espèces dues principalement à l'asynchronicité de réponse des espèces aux perturbations à petite échelle (e.g. chablis), et (ii) un effet positif de la diversité sur la productivité des peuplements, bien que ce dernier soit relativement faible. Pour sa part, DeClerck et al. (2006) n'observent pas de relation entre la diversité des conifères et la *ST* de la productivité de peuplements forestiers de la Sierra Nevada. Selon les auteurs, cette absence de relation pourrait être due au faible gradient de

richesse spécifique considéré (une à quatre espèces), ainsi qu'à la faible asynchronicité des réponses des espèces aux fluctuations environnementales.

S'il est trop tôt pour conclure que la diversité stabilise la productivité des forêts, un certain nombre d'études indirectes confortent, toutefois, l'hypothèse d'une relation diversité-stabilité positive. Tout d'abord, les espèces forestières répondent généralement différemment aux fluctuations environnementales, et notamment aux fluctuations climatiques (Rozas, Lamas & García-González 2009; Drobyshev *et al.* 2013). De ce fait, leurs croissances sont généralement asynchrones. Une augmentation de la diversité pourrait ainsi stabiliser la productivité des peuplements. De plus, la diversité semble augmenter la productivité dans la majorité des forêts du monde (Liang *et al.* 2016). Ce faisant, elle pourrait augmenter la stabilité de leur productivité. Deux mécanismes différents pourraient expliquer l'effet positif de la diversité sur la productivité : (i) la diversité pourrait augmenter la taille et la densité des arbres dans les peuplements via une meilleure imbrication des houppiers (Jucker, Bouriaud & Coomes 2015; Pretzsch & Schütze 2016; Williams *et al.* 2017), et (ii) la diversité pourrait augmenter la croissance individuelle des arbres via des interactions favorables (i.e. compétition réduite et facilitation) entre individus hétérospécifiques (Potvin & Gotelli 2008; Paquette & Messier 2011; Jucker *et al.* 2014b; Chamagne *et al.* 2017). Différentes études suggèrent que ces interactions favorables pourraient également tamponner la réponse des espèces au climat (Lebourgeois *et al.* 2013; Pretzsch, Schütze & Uhl 2013) et ainsi stabiliser la productivité des peuplements, conformément aux observations de Jucker et al. (2014a). Enfin, la diversité pourrait stabiliser la productivité des peuplements en réduisant leur sensibilité à différents types de perturbations comme les tempêtes (Schütz *et al.* 2006), les invasions de pathogènes (Haas *et al.* 2011), ou les épidémies d'insectes phytophages (Jactel & Brockerhoff 2007; Castagneyrol *et al.* 2013).

0.5 Objectifs généraux de la thèse

Cette thèse a trois objectifs principaux :

(i) Tester la relation diversité-stabilité dans les forêts tempérées et boréales de l'Est du Canada. Il s'agit plus spécifiquement d'identifier l'effet de la richesse spécifique sur la stabilité de croissance des forêts.
(ii) Identifier les mécanismes qui gouvernent cette relation diversité-stabilité.
(iii) Déterminer si la richesse spécifique peut stabiliser la croissance des forêts face aux changements climatiques.

Dans cette thèse, seul l'effet stabilisant de la complémentarité des espèces est étudié. Les effets confondants dus aux dynamiques de populations (*effet de sélection* et *dynamiques compensatoires)* sont retirés en travaillant avec des communautés où les populations restent constantes.

0.6 Chapitre 1 : Objectifs et hypothèses

Objectifs : (i) Identifier l'effet de la richesse spécifique sur la stabilité de croissance des forêts tempérées et boréales de l'Est du Canada ; (ii) déterminer le rôle de l'asynchronicité de croissance entre individus dans la relation diversité-stabilité ; (iii) déterminer si la variabilité intraspécifique de réponse aux fluctuations environnementales joue un rôle dans la relation diversité-stabilité.

H1.1 : La diversité stabilise la croissance des forêts.

H1.2 : Cette effet stabilisant est dû, au moins partiellement, à une plus forte asynchronicité de croissance entre individus hétérospécifique qu'entre individus conspécifiques. La diversité réduirait ainsi la variance de croissance des peuplements.

H1.3 : C'est l'asynchronicité de réponses des individus aux fluctuations climatiques qui produit leur asynchronicité de croissance. La variabilité de réponse intraspécifique pourrait donc moduler l'effet stabilisant de la diversité.

0.7 Chapitre 2 : Objectifs et hypothèses

Objectifs : Identifier le rôle des interactions entre individus dans l'effet stabilisant de la diversité sur la croissance des forêts.

H2.1 : Les interactions intraspécifique ont un effet plus négatif sur la croissance des arbres que les interactions interspécifiques. La diversité pourrait donc augmenter la croissance des arbres et ainsi stabiliser la croissance des peuplements.

H2.2 : Les interactions interspécifiques tamponnent la réponse des arbres au climat. La diversité pourrait donc réduire la variance de la croissance des arbres et ainsi stabiliser la croissance des peuplements.

0.8 Chapitre 3 : Objectifs et hypothèses

Objectifs : (i) Déterminer si la richesse spécifique stabilise la croissance des forêts face aux changements climatiques ; (ii) identifier les mécanismes qui contribuent à cet éventuel effet stabilisant.

H3.1 : La diversité stabilise la croissance des peuplements face aux fluctuations climatiques interannuelles (dans le présent comme dans le futur) par le biais de l'asynchronicité de croissance des espèces et des interactions favorables entre individus hétérospécifiques.

H3.2 : La diversité stabilise la croissance des peuplements face aux changements climatiques progressifs (e.g. augmentation des températures) par le biais de l'asynchronicité de croissance des espèces et des interactions favorables entre individus hétérospécifiques.

CHAPITRE 1 : INTRASPECIFIC VARIABILITY IN GROWTH RESPONSE TO ENVIRONMENTAL FLUCTUATIONS MODULATES THE STABILIZING EFFECT OF SPECIES DIVERSITY ON FOREST GROWTH

(LA VARIABILITÉ INTRASPÉCIFIQUE DE RÉPONSE AUX FLUCTUATIONS ENVIRONNEMENTALES MODULE L'EFFET STABILISANT DE LA DIVERSITÉ DES ESPÈCES SUR LA CROISSANCE DES FORETS)

Raphaël Aussenac[1*], Yves Bergeron[1], Claudele Ghotsa Mekontchou[1], Dominique Gravel[2], Kamil Pilch[3], Igor Drobyshev[1,4]

[1] Chaire industrielle CRSNG-UQAT-UQAM en aménagement forestier durable, Institut de recherche sur les forêts, Université du Québec en Abitibi-Témiscamingue (UQAT), 445 boul. de l'Université, Rouyn-Noranda, Québec, J9X 5E4, Canada ; [2] Chaire de recherche en écologie intégrative, Département de biologie, Faculté des sciences, Université de Sherbrooke, 2500 Boulevard Université, Sherbrooke, Québec, J1K 2R1, Canada ; [3] University of Rzeszów, Faculty of Biology and Agriculture, Agroecology Dept., ul. Ćwiklińskiej 1A, 35-601 Rzeszów, Poland; [4] Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, P.O. Box 49, 230 53 Alnarp, Sweden

*Auteur correspondant :
Raphaël Aussenac, Chaire industrielle CRSNG-UQAT-UQAM en aménagement forestier durable, Institut de recherche sur les forêts, Université du Québec en Abitibi-Témiscamingue (UQAT), 445 boul. de l'Université, Rouyn-Noranda, Québec, J9X 5E4, Canada. E-mail : raphael.aussenac@uqat.ca
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1.1 Abstract

1. Differences between species in their response to environmental fluctuations cause asynchronized growth series, suggesting that species diversity may help communities buffer the effects of environmental fluctuations. However, within-species variability of responses may impact the stabilizing effect of growth asynchrony.

2. We used tree ring data to investigate the diversity-stability relationship and its underlying mechanisms within the temperate and boreal mixed woods of Eastern Canada. We worked at the individual tree level to take into account the intraspecific variability of responses to environmental fluctuations.

3. We found that species diversity stabilized growth in forest ecosystems. The asynchrony of species' response to climatic fluctuations and to insect outbreaks explained this effect. We also found that the intraspecific variability of responses to environmental fluctuations was high, making the stabilizing effect of diversity highly variable.

4. *Synthesis*. Our results are consistent with previous studies suggesting that the asynchrony of species' response to environmental fluctuations drives the stabilizing effect of diversity. The intraspecific variability of these responses modulates the stabilizing effect of species diversity. Interactions between individuals, variation in tree size and spatial heterogeneity of environmental conditions could play a critical role in the stabilizing effect of diversity.

Key words: biodiversity, dendrochronology, growth asynchrony, plant-climate interactions, plant-herbivore interactions, plant-plant interactions, plant population and community dynamics, tree growth

1.2 Résumé

1. Les différences entre les espèces dans leur réponse aux fluctuations environnementales produisent des séries de croissance asynchrones, ce qui suggère que la diversité des espèces pourrait permettre aux communautés d'atténuer les effets des fluctuations environnementales. Cependant, la variabilité intra-espèces des réponses pourrait avoir un impact sur l'effet stabilisant de l'asynchronicité de croissance.

2. Nous avons utilisé les données dendrochronologiques afin d'étudier la relation diversité-stabilité et ses mécanismes sous-jacents dans les forêts mixtes tempérées et boréales de l'est canadien. Nous avons travaillé à l'échelle individuelle afin de prendre en considération la variabilité intraspécifique des réponses aux fluctuations environnementales.

3. Nous avons observé que la diversité des espèces stabilisait la croissance dans les écosystèmes forestiers. L'asynchronicité de réponse des espèces aux fluctuations climatiques et aux épidémies d'insectes expliquait cet effet. Nous avons également observé que la variabilité intraspécifique des réponses aux fluctuations environnementales était importante, ce qui rendait l'effet stabilisant de la diversité particulièrement variable.

Synthèse : Nos résultats sont en accord avec les études précédentes suggérant que l'asynchronicité de réponse des espèces aux fluctuations environnementales gouverne l'effet stabilisant de la diversité. La variabilité intraspécifique de ces réponses module l'effet stabilisant de la diversité des espèces. Les interactions entre individus, les différences de taille des arbres et l'hétérogénéité spatiale des conditions environnementales pourraient jouer un rôle déterminant dans l'effet stabilisant de la diversité.

Mots clés : biodiversité, dendrochronologie, asynchronicité de croissance, interactions plante-climat, interactions plante-herbivore, interactions plante-plante, population de plantes et dynamique des communautés, croissance des arbres

1.3 Introduction

Species diversity plays a key role in ecosystem functioning, particularly by stabilizing productivity through time (Loreau *et al.* 2001; Hooper *et al.* 2005; Cardinale *et al.* 2012; Hooper *et al.* 2012). It has been suggested that species diversity may be critical to ensure ecosystem sustainability in the face of environmental fluctuations. Both theoretical (Yachi & Loreau 1999; de Mazancourt *et al.* 2013; Loreau & de Mazancourt 2013) and grassland experiments (Tilman 1999; Isbell, Polley & Wilsey 2009; Hector *et al.* 2010) suggest that differences in species response to environmental fluctuations is the primary mechanism underlying the stabilizing effect of diversity. As a result, these differences generate asynchronous population dynamics (Loreau 2010), enabling productivity compensations among species and thereby promote the stability of the community-level productivity. Interactions among individuals (i.e. competition and facilitation) may, however, modulate the stabilizing effect of diversity. For instance, it has been shown that competition can amplify the asynchrony of population dynamics by promoting the abundance of species which are better adapted to the growing season climate (Gonzalez & Loreau 2009; Mariotte *et al.* 2013). Although there is mounting evidence of the involvement of these factors in the stabilizing effect of diversity, little is known about their respective contributions.

Unlike grasslands, forests offer several advantages to understanding the mechanisms that control the diversity-stability relationship. First, due to the long life span of trees, population dynamics are much slower in forest communities. As a consequence, forest composition cannot change in response to inter-annual environmental fluctuations. The stabilizing effect of diversity in tree communities would, therefore, mainly rely on the asynchrony of individuals' growth and not on the asynchrony of population dynamics. Second, long records of annual growth are available for individual trees through the use of dendrochronology, providing a longer time perspective on the asynchrony of

species response to environmental fluctuations. Finally, unlike grassland communities where individuals are often difficult to define due to the common occurrence of semi-independent parts, trees are easily distinguishable from one another. This feature makes it possible to take into account the variability of individuals' response within species, which may affect the stabilizing effect of diversity. de Mazancourt et al. (2013) has demonstrated analytically, that the stabilizing effect of the asynchrony of species' response to the environment decreases with intraspecific variability of response. This finding is consistent with a study conducted in tree communities (Clark 2010), which demonstrated that species having similar responses to environmental fluctuations may differ in their distributions of individuals' responses. The corollary of this observation is that individuals belonging to species with different (i.e. asynchronous) responses could have similar (i.e. synchronous) responses, which would, therefore, limit the stabilizing effect of the asynchrony of species response. Interactions among individuals and spatial heterogeneity of environmental conditions may be the source of the variability of individuals' response (Cescatti & Piutti 1998; Clark 2010; de Mazancourt *et al.* 2013). As a result, asynchrony of response among species has been shown to be higher between individuals occurring in the same neighbourhoods than within an entire stand (Clark 2010).

Climatic fluctuations (Fritts 1976) and insect outbreaks (Morin *et al.* 2009; Sutton & Tardif 2009) are two major drivers of the inter-annual growth variability of trees in North American forests. Since tree species typically respond differently to climatic fluctuations (Rozas, Lamas & García-González 2009; Drobyshev *et al.* 2013), and since insects may be host specific (Jactel & Brockerhoff 2007; Castagneyrol *et al.* 2013), an increase in tree diversity could help stabilize forest productivity. In the face of insect outbreaks, the stabilizing effect of diversity could not only stem from species differences in their susceptibility to insect attacks, but also from a reduction of herbivory in more diverse forests due to a "host dilution" effect (Jactel & Brockerhoff

2007; Castagneyrol *et al.* 2013). Some recent studies have investigated the diversity-stability relationship in forest ecosystems in the face of extreme climatic events (Pretzsch 2005; Pretzsch, Schütze & Uhl 2013; Jucker *et al.* 2014a) and herbivory (Jactel & Brockerhoff 2007; Castagneyrol *et al.* 2013). They concluded that diversity has a stabilizing effect on the overall productivity of mixed stands.

We used dendrochronological data (1) to determine whether tree species diversity stabilizes productivity in the temperate and boreal mixed woods of Eastern Canada and (2) to identify the mechanisms underlying the stabilizing effect of diversity. We, therefore, paid particular attention to the intraspecific (i.e. among single trees) variability of responses to annual environmental fluctuations, whatever the mechanisms generating this variability. We conducted our analyses on pairs of individuals occurring in the same neighbourhood so that we worked with individuals that were likely to be interacting together and sharing the same micro-environmental conditions. This approach also enabled us to take into account the variability of individuals' response to environmental fluctuations while linking measures of stability to growth asynchrony. We first assessed stability as the inverse of the coefficient of variation (mean/variance) of the total growth of pairs of individuals, and compared it between monospecific and mixed pairs. We hypothesized that (**H1.1**) tree mixture promotes growth stability. We, therefore, expected stability to be higher for pairs of individuals belonging to different species than for pairs of individuals belonging to the same species. Thereafter, we decomposed the effect of diversity on stability into its effect on the mean and the variance of the total growth of pairs of individuals. We hypothesized that (**H1.2**) diversity stabilizes growth by reducing the variance of the total growth of pairs of individuals, and that, because of a higher growth asynchrony among individuals belonging to different species. We, therefore, expected the variance of the total growth to be lower for pairs of individuals belonging to different species than for pairs of individuals belonging to the same species. We also expected

covariance of growth to be lower among individuals belonging to different species than among individuals belonging to the same species. Finally, using multivariate analysis, we identified individuals' response to climatic fluctuations and insect outbreaks. We hypothesized (**H1.3**) that individuals' response asynchrony to environmental fluctuations drove, at least partially, the stabilizing effect of diversity. We, therefore, expected to obtain significant correlations between environmental variables and growth, indicating that individuals' growth variability stemmed from environmental fluctuations and growth asynchrony stemmed from differences in individuals' response to these fluctuations.

1.4 Material and Methods

Data were collected at five 1 ha plots within both temperate and boreal mixed wood stands in Eastern Canada (Figure 1.1). Two boreal mixed wood stands were sampled on the shores of the Lake Duparquet in Western Quebec, which are found within the balsam fir-white birch bioclimatic domain and at 270-275 m above sea level (a.s.l.). These two stands; D1823 (48.45791; 79.23920) and D1847 (48.50398; 79.32084) were both of fire origins established following fires occurring in 1823 and 1847, respectively (Bergeron 2000). Temperate mixed wood stands were sampled at three locations. The first stand, ABI (48.16253; 79.40121), was located in Abitibi, in the balsam fir-white birch domain at the northern limit of the mixed hardwood forest subzone, 375 m a.s.l. The second stand, BIC (48.33361; 68.81771), was located in the St-Lawrence Lowlands, in the balsam fir-yellow birch domain, approximately at 240 m a.s.l. Finally, the third stand, SUT (45.11280; 72.54129) was located in Eastern Townships, in the sugar maple-basswood domain at an elevation ranging between 645 and 690 m a.s.l. The topography was generally flat at all of the sites, except for SUT, which was on a slope facing north-west. The D1823, D1847 and ABI sites were located in the Clay Belt, a large physiographic region in western Quebec and north-eastern Ontario,

characterized by generally thick clay deposits (Veillette 1994). The main soil deposit for the BIC and SUT sites was a glacial till with pockets of organic soil in local depressions.

Climate at the sites ranged from boreal continental, characterized by large variability in temperatures between warm and cold seasons, to a moister temperate climate, characterized by warmer temperatures and more precipitation. The monthly average temperature ranged between -16.9°C in January and 17.3°C in July for the D1823 and D1847 sites over the 1953-2013 period. Annual total precipitation was, on average, 866.6 mm. The temperature was similar at the ABI site (-16.6°C; 17.5°C), but annual precipitation was, on average, higher (894.3 mm). The annual average temperature ranged between -13.3°C in January and 17.1°C in July at BIC, and annual precipitation was, on average, 1050.4 mm. Finally, the SUT site was the warmest and the moistest site with temperatures ranging between -11.6°C in January and 16.9°C in July, and annual precipitation of, on average, 1464.8 mm.

All sites were mature forests stands that were undisturbed by logging, with the exception of the BIC site, which was selectively harvested prior to being designated a National Park in 1984. We considered seven species: eastern white cedar (*Thuja occidentalis* L.), white spruce (*Picea glauca* (Moench) Voss), trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* L.), yellow birch (*Betula alleghaniensis* Britton), red maple (*Acer rubrum* L.), and sugar maple (*Acer saccharum* Marshall).

All trees equal or above 10 cm in diameter at breast height (DBH) were measured (Figure 1.2) and mapped at each site. Tree positions were used to calculate their relative distance for the neighbourhood analyses. We randomly chose 70 individuals per species and per site in five DBH classes for coring. Sampling intensity across DBH classes was stratified to follow the DBH distribution of each species. Two cores were

extracted on the opposite sides of the trunk at breast height for each of the selected trees. Cores were measured at 0.01 mm precision, cross-dated and quality checked following standard dendrochronological methods (Stokes & Smiley 1996; Speer 2010). We removed from the analyses cores with a considerable amount of wood rot making tree ring measurement impossible, yielding a total of 43 to 63 individuals per species and site. The analyses were performed on 2041 cores from 1078 trees (Table 1.1).

We obtained climate data for each site for the time period 1953-2013 using the BioSIM 10.3 software (Régnière 1996; Régnière & St-Amant 2007). BioSIM is a collection of bioclimatic models and daily weather databases, which can generate climate variables at various temporal resolutions, using a user-supplied list of locations. For each site, BioSIM interpolated data from the eight closest weather stations using inverse distance weighting output, while adjusting for differences in latitude, longitude and elevation between the data and sites. We considered monthly mean temperatures, growth season length (period with daily means above 5°C), total monthly precipitation, total monthly snowfall, and monthly mean drought-code, which reflects water content of the deep compact organic layers (Girardin & Wotton 2009).

We detrended growth series to keep only the variability associated with the annual climatic variability and to remove temporal autocorrelation. Detrending was done by first averaging growth series associated with a single tree to obtain single-tree chronologies. We then standardized these single-tree chronologies using a 32-year cubic smoothing spline with a 50% frequency response (Speer 2010). We pre-whitened the resulting series by autoregressive modelling to remove temporal autocorrelation (Cook 1987) and to obtain detrended individual chronologies. We averaged the detrended individual chronologies using a bi-weight robust mean to obtain detrended master chronologies for each species and site. Transformations were performed using the R package *dplR* (Bunn 2008). Detrended individual and master chronologies were

used to analyse the climate-growth relationship, whereas raw individual chronologies were used to investigate individual and species annual growth.

Several insect outbreaks of forest tent caterpillar (*Malacosoma disstria* Hubner.) and spruce budworm (*Choristoneura fumiferana* Clem.) occurred in Eastern Canada during the 1953-2013 period (Morin *et al.* 2009; Sutton & Tardif 2009), causing large reductions in tree diameter growth and suggesting that trees responded more to defoliation events rather than to climate during these periods. We ran the analyses for two versions of chronologies, with and without insect outbreaks. To avoid insect-related signals, we removed periods of forest tent caterpillar outbreaks from aspen chronologies, and periods during which spruce budworm outbreaks occurred from white spruce and balsam fir chronologies.

We identified insect outbreaks in a two step procedure. First, we consulted the large-scale aerial surveys of defoliation, carried out by the *Ministère des Forêts de la Faune et des Parcs,* to obtain approximate outbreak dates (MFFP 2015). Periods of defoliation attributed to forest tent caterpillar and spruce budworm outbreaks all matched periods of abrupt growth reduction observed in the host species raw master chronologies (obtained by averaging individuals' raw chronologies). For each site, we then identified the exact outbreak dates using pointer years. These are years with particularly narrow or large rings observed in multiple tree ring series in a region (Schweingruber 1996). We identified site-specific pointer years for each species as years for which at least 70% of the trees exhibited a variation in their growth of at least 10% as compared to the previous year. We obtained the exact outbreak dates using the negative and positive pointer years enclosing the periods of defoliation-reduced growth in the raw master chronologies of host species.

1.4.1 Statistical Analysis

Temporal stability (TS, Tilman 1999) has been commonly used to measure the stabilizing effect of species diversity on the productivity of a community. It is conventionally measured as the inverse of the coefficient of variation (mean/variance) of the total productivity. The effect of diversity on the stability of the total productivity may be decomposed into its effect on the mean and the variance. Furthermore, the variance of the total productivity may be expressed as the sum of the growth variances and covariances of all species in the community. As a consequence, species having asynchronous growth (i.e. low covariance) will decrease the community *TS*. The productivity variance at the community level could be decomposed further as the sum of the growth variances and covariances of all its constituent individuals. Decomposing variance this way allowed for taking into account the variability of individuals' growth (i.e. growth variances), and to link the measures of *TS* to growth asynchrony among individuals (i.e. growth covariances). To facilitate interpretations, we calculated *TS* on the total radial growth of pairs of individuals occurring in the same neighbourhood (defined as an area within 20 m from a focal tree), following the approach of Clark (2010). Proceeding this way enabled us to express the variance of the total growth, and thus *TS*, from a measure of asynchrony (i.e. covariance). *TS* was thus given by:

$$TS = \frac{\mu_{pair}}{\sqrt{\sigma^2{}_{pair}}} \qquad \text{(eqn 1.1)}$$

where μ_{pair} and σ^2_{pair} were the mean and the variance of the total growth of a pair of individuals and where

$$\sigma^2_{pair} = \sigma^2_i + \sigma^2_j + 2.cov(i,j) \qquad \text{(eqn 1.2)}$$

with *i* and *j*, the growth chronologies of two individuals.

We compared the distributions of *TS*, μ_{pair}, σ^2_{pair}, or *cov(i,j)* obtained for pairs of individuals belonging to the same species to those obtained for pairs of individuals belonging to different species to estimate the effect of species mixture on growth stability, and to understand the mechanisms underlying it. We ran four linear models to disentangle the effect of species mixture from the effect of sites and species based on the following structure:

$$Y = \alpha + MIX + SITE + SP + \varepsilon \qquad \text{(eqn 1.3)}$$

where *Y* was alternately *TS*, μ_{pair}, σ^2_{pair}, and *cov(i,j)*; α - the reference mean; *MIX* - the effect of mixture on the reference mean, indicating whether the measures of *Y* were calculated on trees belonging to the same species or to different species; *SITE* - the effects of sites on the reference mean; *SP* - the effect of species on the reference mean. *SP* is a factorial effect coded as dummy variables with two categories indicating the presence or the absence of each of the seven species in the pairs of individuals.

We expected that distributions of *TS* values obtained for paired individuals belonging to different species would be higher than those obtained for individuals belonging to the same species, indicating a stabilizing effect of mixture on growth. We also expected that distributions of σ^2_{pair}, and *cov(i,j)* values obtained for paired individuals belonging to different species would be lower than those obtained for individuals belonging to the same species, indicating that growth asynchrony is a driver of the stabilizing effect of mixture. We performed these analyses on the 1953-2013 period, both after removing insect outbreak periods from individual chronologies and with insect outbreak periods included. Since tree neighbourhoods could have been different 60 years prior to sampling, we also conducted these analyses on the 1993-2013 period to ensure the

robustness of the results obtained on the 1953-2013 period. In doing so, we assumed changes in tree neighbourhoods to be insignificant during the last 20 years.

To take into account the effect of tree size on *TS*, μ_{pair}, σ^2_{pair}, and *cov(i,j)* on the 1993-2013 period, we added an extra variable (*SIZE*) to equation 1.3. *SIZE* was a categorical variable with three categories, indicating whether pairs of individuals were composed of small trees, a small and a large tree, or two large trees. Categories were based on tree *DBH* in 2011 relative to the median *DBH* of all trees cored on the site. Since *TS*, μ_{pair}, σ^2_{pair}, and *cov(i,j)* were measured on the growth of two individuals (having potentially different sizes) a continuous variable could not be used. We included *SIZE* in the analyses conducted on the 1993-2013 period only, since *DBH* measured in 2011 could not provide a sound estimate of tree sizes prior to 1993. The *SIZE* variable enabled us to account for differences in tree size distribution among species, and between pure and mixed pairs, while estimating the effect of *MIX* on *TS*, μ_{pair}, σ^2_{pair}, and *cov(i,j)*.

We used bootstrapped response functions (Fritts 1976; Guiot 1991) to identify the climatic variables that significantly influenced species growth. In response function analysis, a detrended master chronology of a species (free from insect outbreak signals) was regressed against the principal components obtained on the set of climatic variables. Our rationale to use response functions in this study was twofold. First, we wanted to identify the climatic factors controlling species-specific growth on each site. Second, the response functions were used as a filter to select climatic variables to be introduced in the analysis assessing individuals' response to environmental fluctuations. We ran response functions on site- and species-specific detrended master chronologies and site-specific climate datasets using R package *treeclim* (Zang & Biondi 2015). In these analyses, we used 52 climatic variables of both the year concurrent with and preceding the growth period, starting from June of the year

preceding the ring formation and ending with August of the year concurrent with the ring formation. July and August total snowfalls were not used in the response functions since they were null most of the time. Following the same logic, we only considered drought codes for the periods June through August for the year prior to the growing period, and May through August for the current growing season. We also used growing season lengths for the previous and the current years.

We ran redundancy analysis (RDA) to identify individuals' response to environmental fluctuations and to determine whether the asynchrony of response of individuals belonging to different species contributed to the stabilizing effect of diversity. RDA runs a set of independent multivariate regressions, similar to response functions, but then performs a constrained ordination to position the individuals in a multidimensional space of environmental factors (Legendre & Legendre 2012). The distance between individuals in the ordination indicated the asynchrony in their response to environmental fluctuations among them. Our **H1.3** hypothesis was, therefore, contingent upon obtaining significant RDAs, indicating that environmental fluctuations controlled the variability of individuals' growth. Significant RDAs would, therefore, demonstrate that the asynchrony of individuals' response to environmental fluctuations enabled growth compensations among individuals and thus contributed to the stabilizing effect of species diversity. We ran RDAs on two sets of chronologies, without and with the growth variability caused by insect outbreaks. In the first case, we aimed to consider exclusively the effects of climatic fluctuations on growth. In the second case, we sought to identify tree's response simultaneously to both factors. For these analyses, we added a binary variable indicating the presence of each insect as an additional explanatory variable. The climatic variables used in RDAs were those previously identified in response function analysis. Detrended individual series were considered as response variables, with each annual growth value considered as an observation. RDAs were performed for each site including only years for which all species had growth data for at least 30 individuals. The significance of RDAs was

tested with the F-test of the canonical relationships between growth index values and environmental variables. The explained variance values associated with each RDA provided information on the variability of individuals' response to environmental fluctuations. We computed the RDAs with the R package *rdaTest* (Legendre & Durand 2012).

To determine whether diversity had a stabilizing effect through the reduction of herbivory, we studied the relationship between the intensity of the damages caused by insects to host trees and the diversity in the neighbourhood of host trees in a linear regression. We estimated the intensity of insect attacks as the ratio between the mean growth of trees outside insect outbreak periods and their growth during insect outbreaks. We estimated diversity around trees using the Shannon diversity index which measured diversity as a function of species proportion (p_i) in the community. For $i = 1,\ldots,s$ species within a radius (R=20 m) around a tree, the Shannon diversity index H was given by:

$$H = -\sum_{i=1}^{s} p_i ln\,(p_i) \qquad \text{(eqn 1.4)}$$

where $p_i = ba_i/BA$, with ba_i being the basal area of species i in the neighbourhood and BA being the total basal area in the neighbourhood. We conducted this analysis for trees belonging to the three species susceptible to insect attacks in our sites (*A. balsamea, P. glauca, P. tremuloides*). We expected trees growing in diverse neighbourhoods to be less affected by insect outbreaks.

1.5 Results

Models describing TS, μ_{pair}, σ^2_{pair}, and $cov(i,j)$ as a function of mixture (equation 1.3) showed the same trends in both the 1953-2013 (Table 1.2) and 1993-2013 (see Table

1.S1 in Supporting information) periods. *TS* was significantly higher for pairs of individuals belonging to different species than for pairs of individuals belonging to the same species, indicating a stabilizing effect of species mixture (i.e. diversity) on growth (Figure 1.3 and Table 1.2). In contrast, μ_{pair} (Figure 1.S1), σ^2_{pair} (Figure 1.S2), and *cov(i,j)* (Figure 1.S3) were significantly lower for pairs of individuals belonging to different species than for pairs of individuals belonging to the same species, as indicated by the negative and significant parameters associated with the *MIX* variable in the model (Table 1.2).

Insect outbreaks amplified the effect of mixture on *TS*, σ^2_{pair}, and *cov(i,j)*. The stabilizing effect of mixture was higher when the signal from insect outbreaks was preserved in the chronologies (*MIX* = 0.80) as compared to chronologies with no insect outbreak signal (*MIX* = 0.52; Table 1.2). The negative effect of mixture on σ^2_{pair} and *cov(i,j)* was stronger when insect outbreaks were preserved in the chronologies (*MIX* =-0.61, -0.15 respectively) as compared to chronologies without them (*MIX* = -0.44, -0.10 respectively; Table 1.2). In contrast, insect outbreaks slightly decreased the negative effect of mixture on μ_{pair} (Table 1.2).

Tree size increased *TS* (Table 1.S1), although its effect was limited when the signal from insect outbreaks was preserved. Pairs of large trees had higher $\mu_{pair.}$ Pairs composed of a small and a large tree had lower both *cov(i,j)* and σ^2_{pair}, as compared to pairs of trees of the same size (large or small). However, the effect of tree size on σ^2_{pair} was weak, about five to ten times lower than the effect of *MIX*.

Response functions showed that the climatic conditions (temperature, precipitation and drought code) of summer months (June to August) of the current growing season were the most influential to growth across species and sites (Table 1.3). In contrast, we found few significant correlations between species growth and climatic conditions of the

autumn of the previous growing season and the early winter (October to February). The northernmost sites (D1823 and D1847) showed a more pronounced global effect of climatic conditions of summer months of the previous growing season on species growth than all of the other sites. We observed some asynchrony between conifers and deciduous species response to climate. For example, on the BIC site, while growth of all deciduous species significantly correlated to current summer drought (i.e. to drought code), this was not the case for balsam fir. Similarly, on the D1823 site, while all conifers growth significantly correlated to current summer drought, the growth of trembling aspen did not.

RDAs showed that the asynchrony of response to environmental fluctuations of individuals' belonging to different species contributed to the stabilizing effect of diversity by enabling growth compensation among individuals (Figure 1.4). All RDAs were significant except RDAs performed on chronologies free from insect outbreak signals for the D1823 and D1847 sites (Figure 1.4a). However, rather than a lack of correlation between environmental fluctuations and growth, this could be due to the relatively short period on which these RDAs were performed (24 and 29 years for the D1823 and D1847 sites, respectively), after removing the 4 years of forest tent caterpillar outbreak, the 17 years of spruce budworm outbreak, and years for which not all species had growth data for at least 30 individuals. Species-specific ellipses, however, overlapped broadly, despite distinct locations of centroids (i.e. distinct average responses), indicating that species could have close responses to environmental fluctuations. The explained variance for RDAs ranged from 8.6 to 25.6%, indicating that the variability of individuals' response to environmental fluctuations was high.

We found no significant relationship between the intensity of the damages caused by insects to host trees and the diversity in the neighbourhood of host trees (Table 1.4).

1.6 Discussion

Our results showed that diversity stabilized growth in forest ecosystems, supporting the **H1.1** hypothesis. The stabilizing effect of diversity stemmed from a higher growth asynchrony among individuals belonging to different species, which reduced the variance of the total growth of pairs of individuals, supporting the **H1.2** hypothesis. The asynchrony of response to environmental fluctuations of trees belonging to different species contributed to the stabilizing effect of diversity, by controlling the growth asynchrony of trees, supporting the **H1.3** hypothesis. However, the intraspecific variability of response to environmental fluctuations was high, generating a broad overlap of species responses despite differences in their average responses (Figure 1.4). This demonstrates the interest of working at the individual-level rather than at the species-level. These results were persistent regardless of whether the forest was temperate or boreal mixed, and in the face of different types of environmental fluctuations (climatic fluctuations and insect outbreaks).

We demonstrated that in forest ecosystems, even when controlling for population dynamics, tree species diversity could stabilize productivity through the asynchrony of responses to climatic fluctuations and insect outbreaks of individuals' belonging to different species. The asynchrony of individuals' response enabled growth compensation among individuals that ultimately produced a stabilizing effect. These results are consistent with previous studies in forest ecosystems (Jucker *et al.* 2014a) and grassland communities (Tilman 1999; Isbell, Polley & Wilsey 2009; Hector *et al.* 2010), suggesting that the asynchrony of species response is a mechanism driving the stabilizing effect of diversity.

The stabilizing effect of species mixing was stronger in analyses including both climate and insect outbreak effects, as compared to the analyses operating on chronologies with insect signal removed. We explain that by species differences in their susceptibility to

insects and the resulting asynchronized growth series. We speculate that the stabilizing effect of diversity could be further enhanced through (1) a reduction in the outbreak-related mortality both for host and non-host species (Bouchard, Kneeshaw & Bergeron 2005), and (2) the increase in the abundance of the insect natural enemies, limiting herbivory (Cappuccino *et al.* 1998). However, higher neighbourhood diversity did not reduce the insect-induced growth decline of host species during outbreaks, as it has been shown earlier (Jactel & Brockerhoff 2007; Castagneyrol *et al.* 2013). This divergence of results could stem from a difference in the scale of observation. Previous studies were done at the stand level while our study was carried out on a smaller neighbourhood level. Good dispersal abilities of forest tent caterpillar and spruce budworm (Greenbank 1957) could make the induced damage depend on the availability of their host at the stand and regional scales rather than at the neighbourhood scale.

We found a negative effect of diversity on the mean of the total growth of tree pairs. This outcome is contrary to both theoretical predictions and empirical results (Tilman 1999; Yachi & Loreau 1999; Isbell, Polley & Wilsey 2009; Hector *et al.* 2010; de Mazancourt *et al.* 2013; Loreau & de Mazancourt 2013; Chamagne *et al.* 2017), which have shown that diversity usually increases productivity, in particular through a better resource partitioning between species having different niches. The negative effect of diversity on the mean of the total growth of tree pairs could be an artefact arising due to the fact that we have trees of all sizes (Figure 1.2). Radial growth typically initially increases with tree size before decreasing in larger trees. Comparing the total growth of a pair of intermediate-sized firs (growing rapidly) to a pair consisting of a fir and a birch, both of small size (growing slowly), for instance, would lead to the conclusion that diversity has a negative effect on growth, while it would actually be a size effect. Our analysis conducted on the 1993-2013 period confirmed that tree size influenced *TS*, essentially by impacting the mean growth of tree pairs. The wide range of tree sizes in our data therefore prevented us from concluding on the effect of diversity on the mean of the total growth of tree pairs. Nevertheless, the negative effect of diversity on

the mean of the total growth of tree pairs indicates that diversity stabilized growth by reducing the total growth variance, and not because of a positive effect on the total growth mean.

The intraspecific variability of response to environmental fluctuations was high, leading to a highly variable effect of species mixture on *TS* among tree pairs. This variability could stem from interactions among individuals, such as competition and facilitation, and the spatial heterogeneity of environmental conditions (Cescatti & Piutti 1998; Clark 2010; de Mazancourt *et al.* 2013). By modulating individuals' response to environmental fluctuations, these two factors would affect the growth variability of individuals, their growth covariance and, therefore, the variance in the total growth of tree pairs. This outcome is complementary to the findings of Morin et al. (2014) who demonstrated, using virtual experiments based on a forest succession model, that the stabilizing effect of diversity in forest ecosystems was mainly driven by the asynchrony of species response to small disturbances rather than to environmental fluctuations. In our mixed stands, most individuals were in immediate vicinity of trees of different species. Since pairs of individuals may interact with other individuals belonging to different species, our approach did not allow us to directly investigate the role of among-tree interactions on the stabilizing effect of diversity. This observation does not question the fact that interactions, size and micro-environment could modulate the stabilizing effect of diversity. Furthermore, we assume that no systematic bias due to neighbouring trees were introduced in the estimation of the effect of diversity on *TS* and its components, since trees were sampled randomly. Our study calls for further analyses of the mechanisms underlying the intra-specific variability of response to environmental fluctuations.

Our work highlights the value of working in forest communities to study the mechanisms driving the diversity-stability relationship. This is especially valuable since it gives us access to the individual-level where growth compensation actually

occurs, while eliminating the influence of population dynamics. We showed that diversity increased the stability of growth in forest ecosystems and that the asynchrony of response to environmental fluctuations of individuals' belonging to different species contributed to this stabilizing effect. Mechanisms at the origin of the variability of individuals' response, such as interactions between individuals and spatial heterogeneity of environmental conditions, could, therefore, play a crucial role in the stabilizing effect of diversity.

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1.9 Tables

Tab. 1.1: Number of trees cored per species and site. The number of cores are shown in brackets.

Site	D1823	D1847	ABI	BIC	SUT
A. balsamea	48 (84)	51 (96)	58 (104)	63 (107)	54 (91)
P. glauca	47 (94)	58 (109)	47 (93)	-	-
T. occidentalis	52 (98)	54 (110)	49 (96)	-	-
A. rubrum	-	-	52 (98)	61 (126)	-
A. saccharum	-	-	55 (107)	59 (121)	59 (106)
B. alleghaniensis	-	-	-	-	43 (77)
P. tremuloides	54 (107)	52 (101)	-	62 (116)	-

Tab. 1.2: Summary of the four linear models describing *TS*, μ_{pair}, σ^2_{pair}, and *cov(i,j)* as a function of mixture, controlling for species and site effects on the 1953-2013 period. α is the mean of *TS* measures calculated on pairs of individuals comprising at least one white cedar on the ABI site. We ran the model both after removing insect outbreak periods from individual chronologies (a) and with insect outbreak periods included (b).[1] Level of significance: *** < 0.001; ** < 0.01; * < 0.05; ns = not significant (> 0.05).

	TS		$\sigma^2_{\pi\alpha\iota\rho}$		$\mu_{\pi\alpha\iota\rho}$		*cov(i,j)*	
	(a) Without insect outbreaks[1]	(b) With insect outbreaks[1]	(a) Without insect outbreaks[1]	(b) With insect outbreaks[1]	(a) Without insect outbreaks[1]	(b) With insect outbreaks[1]	(a) Without insect outbreaks[1]	(b) With insect outbreaks[1]
α	3.044***	2.847***	1.154***	1.293***	2.75***	2.692***	0.201***	0.244***
MIX	0.516***	0.804***	-0.439***	-0.606***	-0.377***	-0.341***	-0.105***	-0.152***
$SITE_{BIC}$	0.097***	0.077**	-0.395***	-0.364***	-0.534***	-0.476***	-0.105***	-0.022***
$SITE_{D1823}$	0.068*	-0.123***	-0.37***	-0.276***	-0.473***	-0.477***	-0.03***	-0.012*
$SITE_{D1847}$	0.252***	0.031 ns	-0.43***	-0.404***	-0.533***	0.57***	-0.037***	-0.021***
$SITE_{SUT}$	-0.495***	-0.428***	0.119***	0.216***	-0.145***	-0.055*	-0.003 ns	0.001 ns
SP_{Ab}	-0.063*	-0.551***	0.448***	0.566***	0.729***	0.582***	0.031***	0.06***
SP_{Ar}	-0.407***	-0.699***	0.111***	0.216***	-0.032 ns	-0.059**	0.003 ns	0.026***
SP_{As}	-0.841***	-1.007***	0.066***	0.127***	-0.347***	-0.331***	-0.001 ns	0.014***
SP_{Ba}	-0.317***	-0.505***	1.012***	1.077***	1.036***	1.02***	0.083***	0.098***
SP_{Pg}	-0.629***	-0.697***	0.639***	0.631***	0.674***	0.622***	0.063***	0.076***
SP_{Pt}	-0.316***	-0.736***	0.477***	0.722***	0.853***	0.844***	0.042***	0.079***
Adj-R^2	0.173	0.164	0.242	0.257	0.349	0.319	0.071	0.111
p-value	< 2.2e-16	< 2.2e-16	< 2.2e-16	< 2.2e-16	< 2.2e-16	< 2.2e-16	< 2.2e-16	< 2.2e-16

Tab. 1.3: Site and species-specific climatic variables identified by bootstrapped response function as having a significant correlation with growth. Drought code (DC), temperature (T), precipitation (P), snowfall (S), growth season length (GSL). GSL in previous June correspond to the previous year GSL. The sign (+/-) indicates the direction of the correlation.

		previous year							current year							
Site	Sp	jun	jul	aug	sep	oct	nov	dec	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG
D1823	Ab														DC-	
	Pg		DC-		DC+									P+	DC-	
	Pt			T-							S+					
	To									T-				T-		T-
D1847	Ab	P+										T+				
	Pg		P+									T+				
	Pt			DC-							S+					
	To			T-	S-				S-					T-		P+
ABI	Ab	GSL-														
	Pg												DC+	T-		T-
	To					P-								T-		P+
	Ar		T-								T+					
	As												T-	S-	DC- P+	DC-
BIC	Ab	GSL-			T- S+											
	Pt										S-			P+	DC-	
	Ar										S-			P+	DC-	
	As													P+	DC-	
SUT	Ab						S-							S+		
	As													DC-		
	Ba					P+						S+				

Tab. 1.4: Regressions between the intensity of the damages caused by insects to host trees and the diversity in the host tree neighbourhood. [1]Level of significance: *** < 0.001; ns = not significant (> 0.05). Host species are coded with their initials: Ab (*A. balsamea*), Pg (*P. glauca*), Pt (*P. tremuloides*).

	Ab	Pg	Pt
intercept	2.366 [1]***	2.553 [1]***	3.11 [1]***
slope	-0.093 [1]ns	-0.554 [1]ns	0.286 [1]ns
adjusted R^2	-0.004	0.024	0
p-value	0.763	0.07	0.307

1.10 Figures

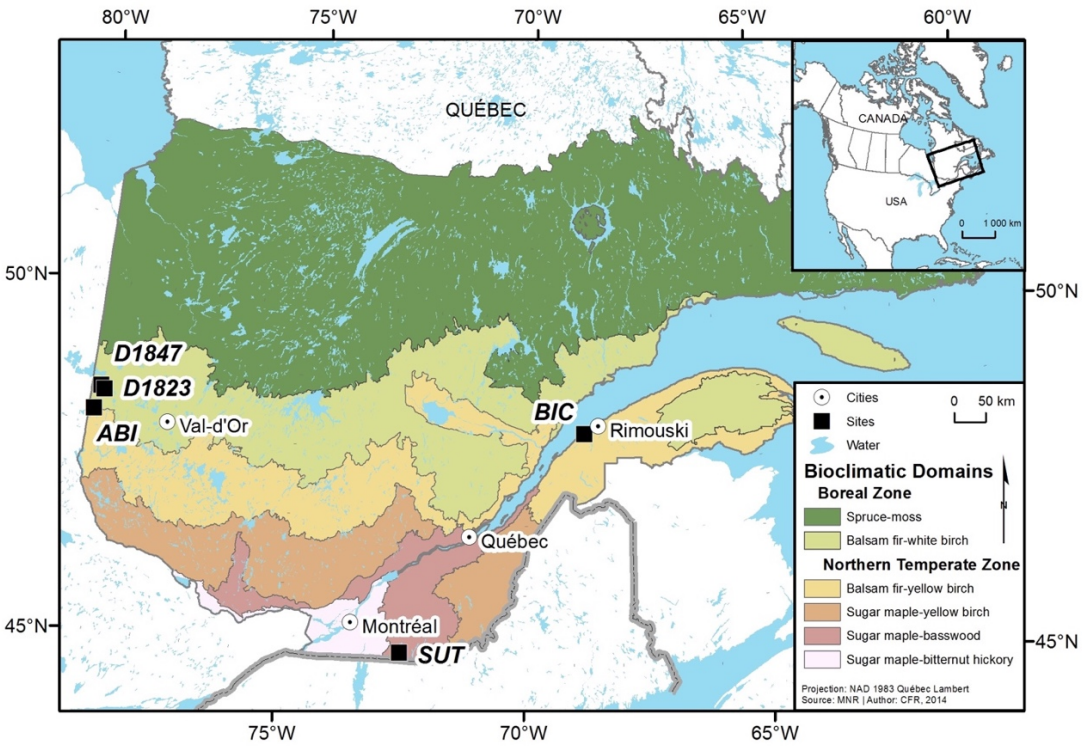

Fig. 1.1: Study sites and bioclimatic domains of Québec.

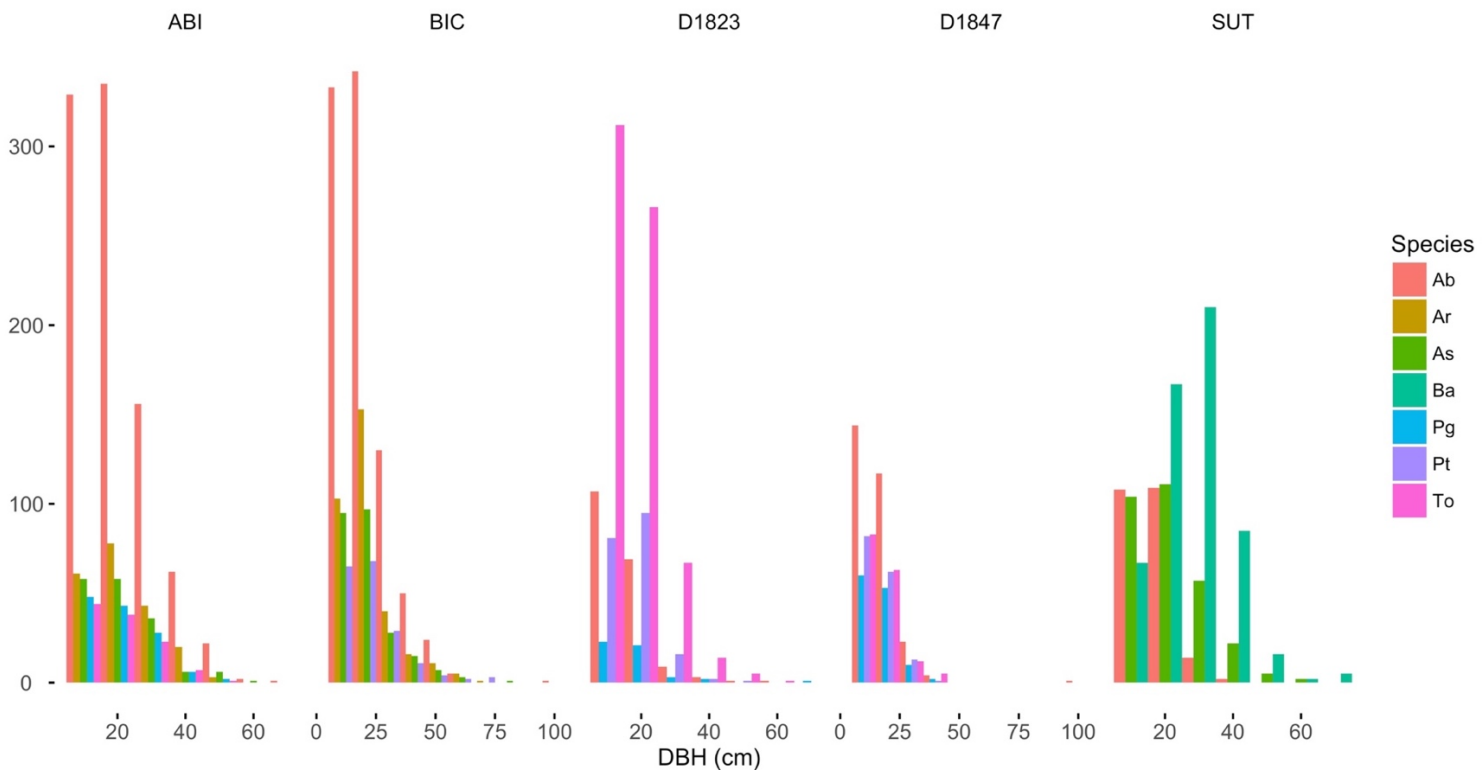

Fig. 1.2: Species and site-specific distributions of tree diameters at study sites.

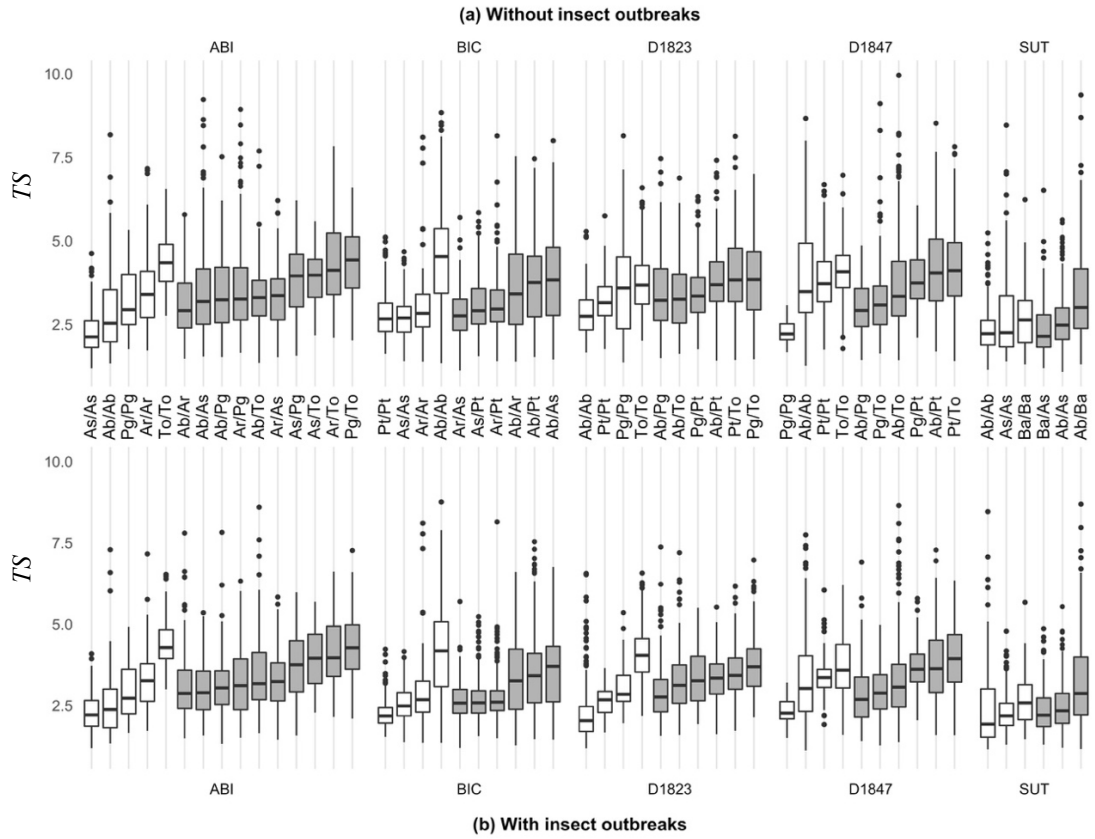

Fig. 1.3: Site and species-specific distributions of TS values measured on paired individuals occurring in the same neighbourhoods. White boxes refer to distributions of *TS* values measured on individuals belonging to the same species, while grey boxes refer to distributions of *TS* values measured on individuals belonging to different species. Distributions were developed both after removing insect outbreak periods from individual chronologies (a) and with insect outbreak periods included (b). Labels indicate to which species the individuals belonged to for each distribution. Species are coded with their initials: Ab (*A. balsamea*), Ar (*A. rubrum*), As (*A. saccharum*), Ba (*B. alleghaniensis*), Pg (*P. glauca*), Pt (*P. tremuloides*), To (*T. occidentalis*).

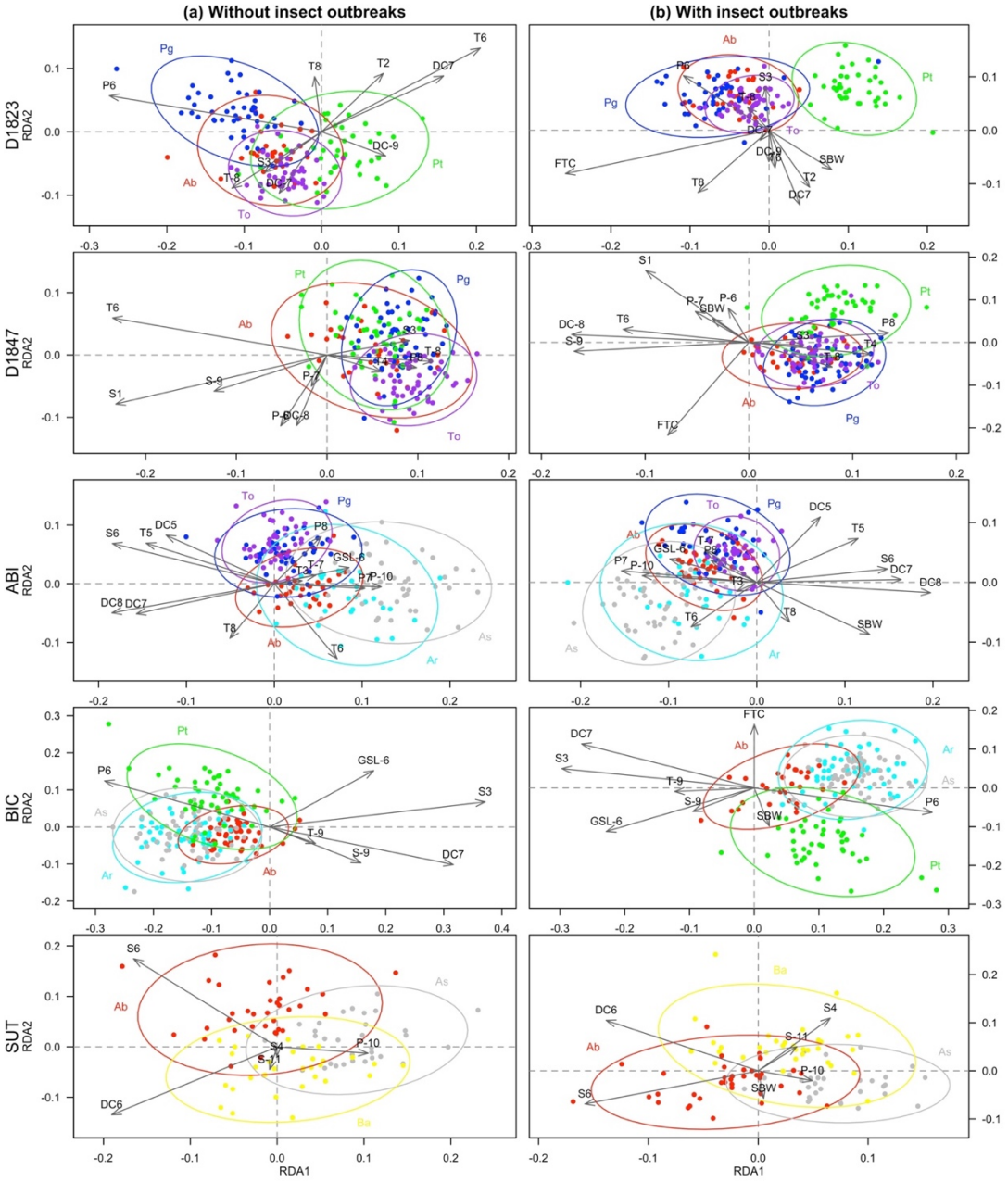

Fig. 1.4: Site-specific redundancy analysis (RDA) performed with individual standardized chronologies, climatic variables and binary variables indicating the presence of insects. Points correspond to individual chronologies. Species-specific ellipses containing 95% of species individuals are shown and identified with species initials.

1.11 Supplementary information

Tab. 1.S1: Summary of the four linear models describing *TS*, σ^2_{pair}, μ_{pair} and *cov(i,j)* as a function of mixture, controlling for species , tree size and sites effects over 1993-2013.

Fig. 1.S1: Site and species-specific distributions of the mean of the total growth of individuals measured on paired individuals occurring in the same neighbourhoods.

Fig. 1.S2: Site and species-specific distributions of the variance of the total growth of individuals measured on paired individuals occurring in the same neighbourhoods.

Fig. 1.S3: Site and species-specific distributions of growth covariance among individuals measured on paired individuals occurring in the same neighbourhoods.

Tab. 1.S1: Summary of the four linear models describing *TS*, σ^2_{pair}, μ_{pair} and *cov(i,j)* as a function of mixture, controlling for species, tree size and sites effects over 1993-2013. α is the mean of *TS* measures calculated on pairs of individuals comprising at least one white cedar on the ABI site. We ran the model both after removing insect outbreak periods from individual chronologies (a) and with insect outbreak periods included (b).1 Level of significance: *** < 0.001; ** < 0.01; * < 0.05; ns = not significant (> 0.05).

	TS		$\sigma^2_{\pi\alpha\iota\rho}$		$\mu_{\pi\alpha\iota\rho}$		*cov(i,j)*	
	(a) Without insect outbreaks[1]	(b) With insect outbreaks[1]	(a) Without insect outbreaks[1]	(b) With insect outbreaks[1]	(a) Without insect outbreaks[1]	(b) With insect outbreaks[1]	(a) Without insect outbreaks[1]	(b) With insect outbreaks[1]
α	4.018***	3.945***	0.602***	0.685***	2.614***	2.56***	0.099***	0.131***
MIX	0.634***	0.894***	-0.259***	-0.376***	-0.312***	-0.279***	-0.051***	-0.089***
$SITE_{BIC}$	-0.215***	-0.072*	-0.117***	-0.151***	-0.471***	-0.439***	0 ns	-0.005 ns
$SITE_{D1823}$	-0.314***	-0.608***	-0.158***	-0.089***	-0.694***	-0.618***	0.001 ns	0.012***
$SITE_{D1847}$	-0.555***	-0.592***	-0.161***	-0.13***	-0.84***	-0.777***	-0.002 ns	0.008**
$SITE_{SUT}$	-1.012***	-0.972***	0.227***	0.21***	-0.055*	-0.044 ns	0.016***	0.01**
$SIZE_{small/large}$	0.113***	0.077**	-0.026**	-0.009 ns	0.014 ns	0.008 ns	-0.015***	-0.009***
$SIZE_{large/large}$	0.212***	0.052 ns	0.022*	0.065***	0.2***	0.189***	0.001 ns	0.013***
SP_{Ab}	0.166***	-0.003 ns	0.337***	0.38***	1.051***	1.058***	0.029***	0.041***
SP_{Ar}	-0.546***	-0.791***	0.112***	0.185***	-0.072**	-0.064*	0.004 ns	0.022***
SP_{As}	-0.902***	-1.108***	-0.081***	-0.031*	-0.652***	-0.644***	-0.017***	-0.004 ns
SP_{Ba}	-0.439***	-0.614***	0.366***	0.433***	0.488***	0.481***	-0.007 ns	0.014*
SP_{Pg}	-0.93***	-0.912***	0.397***	0.412***	0.416***	0.453***	0.032***	0.037***
SP_{Pt}	-0.491***	-1.545***	0.391***	0.666***	0.945***	0.708***	0.042***	0.081***
Adj-R^2	0.1836	0.2891	0.1968	0.2484	0.4198	0.4141	0.07996	0.1458
p-value	< 2.2e-16	< 2.2e-16	< 2.2e-16	< 2.2e-16	< 2.2e-16	< 2.2e-16	< 2.2e-16	< 2.2e-16

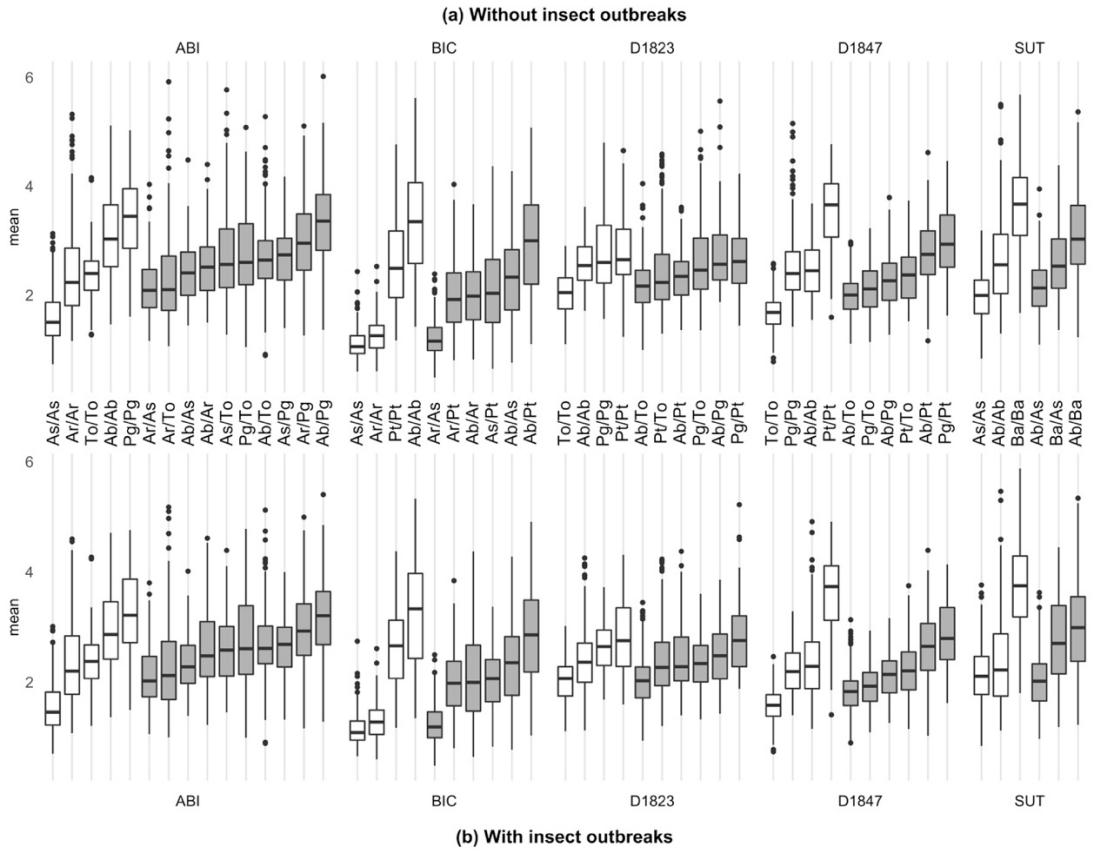

Fig. 1.S1: Site and species-specific distributions of the mean of the total growth of individuals measured on paired individuals occurring in the same neighbourhoods. White boxes refer to distributions of mean values measured on individuals belonging to the same species, while grey boxes refer to distributions of mean values measured on individuals belonging to different species. Distributions were developed both after removing insect outbreak periods from individual chronologies (a) and with insect outbreak periods included (b). Labels indicate to which species the individuals belonged to for each distribution. Species are coded with their initials: Ab (*A. balsamea*), Ar (*A. rubrum*), As (*A. saccharum*), Ba (*B. alleghaniensis*), Pg (*P. glauca*), Pt (*P. tremuloïdes*), To (*T. occidentalis*).

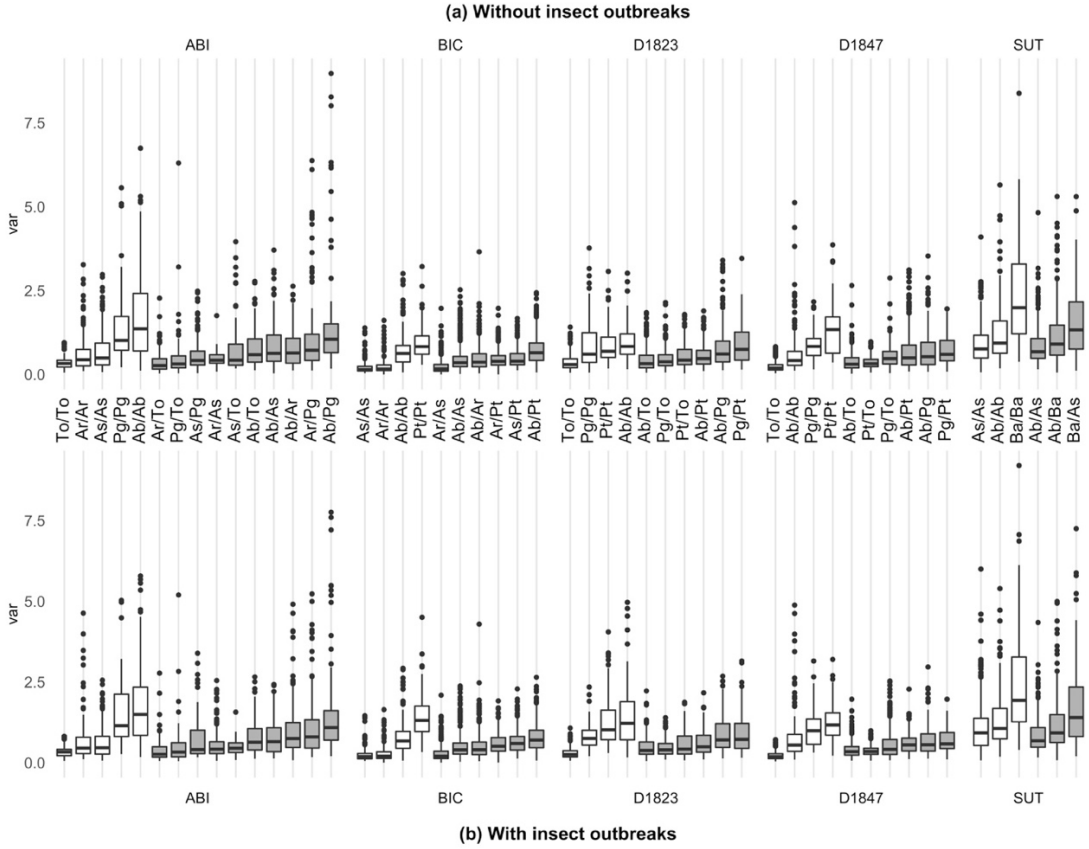

Fig. 1.S2: Site and species-specific distributions of the variance of the total growth of individuals measured on paired individuals occurring in the same neighbourhoods. White boxes refer to distributions of variance values measured on individuals belonging to the same species, while grey boxes refer to distributions of variance values measured on individuals belonging to different species. Distributions were developed both after removing insect outbreak periods from individual chronologies (a) and with insect outbreak periods included (b). Labels indicate to which species the individuals belonged to for each distribution. Species are coded with their initials: Ab (*A. balsamea*), Ar (*A. rubrum*), As (*A. saccharum*), Ba (*B. alleghaniensis*), Pg (*P. glauca*), Pt (*P. tremuloïdes*), To (*T. occidentalis*).

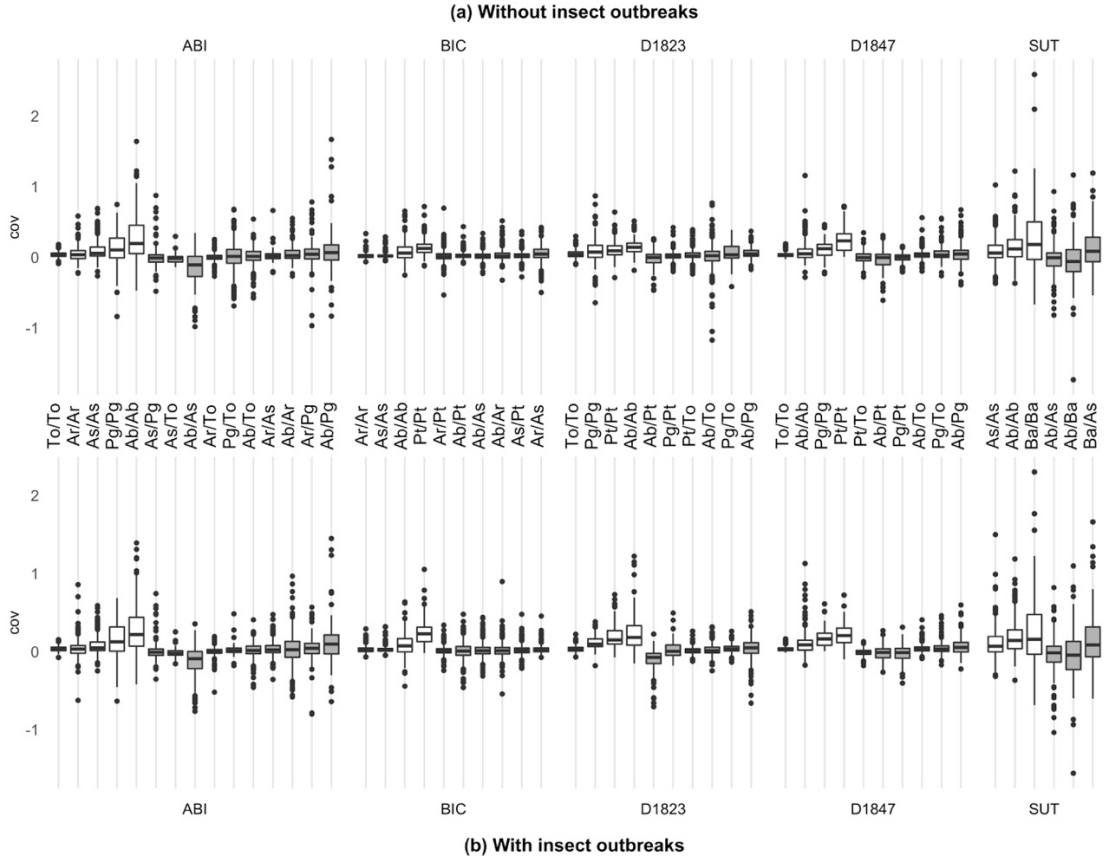

Fig. 1.S3: Site and species-specific distributions of growth covariance among individuals measured on paired individuals occurring in the same neighbourhoods. White boxes refer to distributions of covariance values measured on individuals belonging to the same species, while grey boxes refer to distributions of covariance values measured on individuals belonging to different species. Distributions were developed both after removing insect outbreak periods from individual chronologies (a) and with insect outbreak periods included (b). Labels indicate to which species the individuals belonged to for each distribution. Species are coded with their initials: Ab (*A. balsamea*), Ar (*A. rubrum*), As (*A. saccharum*), Ba (*B. alleghaniensis*), Pg (*P. glauca*), Pt (*P. tremuloïdes*), To (*T. occidentalis*).

CHAPITRE 2 : INTERACTIONS AMONG TREES: A KEY ELEMENT IN THE STABILIZING EFFECT OF SPECIES DIVERSITY ON FOREST GROWTH

(LES INTERACTIONS ENTRE ARBRES : UN ÉLÉMENT CLÉ DANS L'EFFET STABILISANT DE LA DIVERSITÉ DES ESPÈCES SUR LA CROISSANCE DES FORÊTS)

Raphaël Aussenac[1*], Yves Bergeron[1], Dominique Gravel[2], Igor Drobyshev[1,3]

[1] Chaire industrielle CRSNG-UQAT-UQAM en aménagement forestier durable, Institut de recherche sur les forêts, Université du Québec en Abitibi-Témiscamingue (UQAT), 445 boul. de l'Université, Rouyn-Noranda, Québec, J9X 5E4, Canada ; [2] Chaire de recherche en écologie intégrative, Département de biologie, Faculté des sciences, Université de Sherbrooke, 2500 Boulevard Université, Sherbrooke, Québec, J1K 2R1, Canada ; [3] Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, P.O. Box 49, 230 53 Alnarp, Sweden

*Auteur correspondant :
Raphaël Aussenac, Chaire industrielle CRSNG-UQAT-UQAM en aménagement forestier durable, Institut de recherche sur les forêts, Université du Québec en Abitibi-Témiscamingue (UQAT), 445 boul. de l'Université, Rouyn-Noranda, Québec, J9X 5E4, Canada. E-mail : raphael.aussenac@uqat.ca

2.1 Abstract

There is mounting evidence that species diversity stabilizes the productivity of plant communities through, among other factors, species differences in their response to environmental fluctuations. In annual plant communities, these differences generate asynchronous population dynamics which enable compensation among species and thereby stabilize productivity at the community level. Interactions among individuals have been shown to further promote stability by amplifying the asynchrony of population dynamics. In forest ecosystems, however, the stabilizing effect of diversity may rely on the asynchrony of tree growth rather than on population dynamics. Under these conditions, the role of interactions in the stabilizing effect of diversity remains unclear. We used tree-ring width chronologies from temperate and boreal mixed woods of Eastern Canada to identify the role of interactions among individuals in the stabilizing effect of diversity on forest productivity. We found that diversity promoted tree growth and buffered tree response to drought. These outcomes indicate that diversity, through favorable interactions, may increase the mean and reduce the variance of tree growth, which may ultimately increase the stability of forest productivity. Our study helps better understand the mechanisms underlying the stabilizing effect of diversity in forest ecosystems and demonstrates that interactions among individuals contribute to this effect.

Key words: biodiversity, interactions, dendrochronology, ecosystem functioning, stability, tree growth

2.2 Résumé

Un nombre croissant d'études suggère que la diversité des espèces stabilise la productivité des communautés végétales par le biais, notamment, des différences de réponses des espèces aux fluctuations environnementales. Dans les communautés de plantes annuelles, ces différences génèrent des dynamiques de populations asynchrones qui permettent des compensations entre espèces et ainsi stabilisent la productivité à l'échelle des communautés. Les interactions entre individus pourraient augmenter encore davantage la stabilité des communautés en amplifiant l'asynchronicité des dynamiques de populations. Dans les écosystèmes forestiers, cependant, l'effet stabilisant de la diversité pourrait dépendre de l'asynchronicité de croissance des arbres plutôt que des dynamiques de populations. Dans ces conditions, le rôle des interactions dans l'effet stabilisant de la diversité reste à éclaircir. Nous avons utilisé des chronologies de la largeur des cernes provenant de forêts mixtes tempérées et boréales de l'Est du Canada pour identifier le rôle des interactions entre individus dans l'effet stabilisant de la diversité sur la productivité forestière. Nous avons observé que la diversité favorisait la croissance des arbres et tamponnait la réponse des arbres à la sécheresse. Ces résultats indiquent que la diversité, grâce à des interactions favorables, peut augmenter la moyenne et réduire la variance de la croissance des arbres, ce qui pourrait ultimement augmenter la stabilité de la productivité forestière. Notre étude aide à mieux comprendre les mécanismes qui sous-tendent l'effet stabilisant de la diversité dans les écosystèmes forestiers et démontre que les interactions entre individus contribuent à cet effet.

Mots clés : biodiversité, compétition, dendrochronologie, fonctionnement des écosystèmes, facilitation, croissance des arbres

2.3 Introduction

Species diversity (here after diversity) has been found to stabilize ecosystem productivity under fluctuating environmental conditions (Hector *et al.* 2010; Jucker *et al.* 2014a; Morin *et al.* 2014). The stabilizing effect of diversity mainly relies on the differences in species-specific response to environmental fluctuations. These differences generate asynchronous population dynamics and thereby promote the temporal stability of the community-level productivity (Loreau & de Mazancourt 2008; de Mazancourt *et al.* 2013; Loreau & de Mazancourt 2013). Interactions among individuals may also modulate the stabilizing effect of diversity by affecting population dynamics. In grasslands, for instance, interactions have been shown to increase the abundance of species which are better adapted to the growing season conditions. As environmental conditions change from one year to another, interactions may, therefore, amplify the asynchrony of population dynamics and thereby contribute to the stabilizing effect of diversity on community productivity (Mariotte *et al.* 2013). In tree communities, however, composition does not change in response to rapid environmental fluctuations, such as annual climatic fluctuations, due to the long-life span of trees. Over short periods (relative to the lifespan of trees) populations may, therefore, remain constant in forest stands. As a consequence, the stabilizing effect of diversity in tree communities would mainly rely on the asynchrony of individuals' growth response to environmental fluctuations (Jucker *et al.* 2014a; Aussenac *et al.* 2017), rather than on the asynchrony of population dynamics. Under these conditions, i.e. in the absence of population dynamics, the role of interactions in the stabilizing effect of diversity remains unclear.

Temporal stability (TS; Tilman 1999), measured as the inverse of the coefficient of variation (mean/variance) of a community total productivity, has been commonly used to assess the stabilizing effect of diversity. The effect of diversity on *TS* may be

decomposed into its effect on the mean and the variance of the total community productivity. In turn, the mean of the total productivity may be further decomposed as the sum of the mean growth of all individuals in the community, and its variance computed as the sum of the growth variances and covariances of all individuals in the community (Aussenac *et al.* 2017). Any factor affecting one of the three components of *TS* (mean, variance and covariance) may, therefore, impact the *TS* of forest productivity.

Interactions among individuals could impact the stabilizing effect of diversity in forest ecosystems by affecting the mean and variance of tree growth. Indeed, diversity has been shown to increase tree mean growth (Potvin & Gotelli 2008; Jucker *et al.* 2014b; Chamagne *et al.* 2016; Chen *et al.* 2016; Fichtner *et al.* 2017), and to reduce the variance of tree growth by buffering tree response to climate fluctuations (Lebourgeois *et al.* 2013; Pretzsch, Schütze & Uhl 2013; Jucker *et al.* 2014a). These effects of diversity on the mean and variance of tree growth were explained by facilitation and reduced competition among heterospecific individuals. Such favorable interactions (facilitation and reduced competition) arise from species complementarity (Cardinale *et al.* 2007), which is usually interpreted as species differences in their ecological niches, functional traits and strategies for resource uptake and use. Although the effects of diversity on the mean and variance of tree growth have already been documented separately, this study is, to our knowledge, the first considering both effects simultaneously. Furthermore, the impact of interactions on individuals' response to environmental fluctuations has never been accounted for in the diversity-stability relationship neither in theory nor in empirical studies.

We used tree-ring width chronologies from temperate and boreal mixed woods of Eastern Canada to identify the role of interactions among individuals in the stabilizing effect of diversity on forest productivity. For that, we measured the effect of diversity

on tree growth and on tree response to drought. We used mixed models to describe tree growth as a function of tree size, summer drought, diversity and an interaction between diversity and summer drought, while controlling for the effects of site, species and composition. Based on the concept of species complementarity, consistent with coexistence theory (Chesson 2000), we hypothesized (**H2.1**) that interspecific interactions would be more beneficial to growth than intraspecific interactions. We therefore expected diversity to promote tree growth. We also hypothesized (**H2.2**) that trees surrounded by heterospecific neighbors would be less sensitive to drought than trees surrounded by conspecific neighbors. This lower sensitivity to summer drought would arise from species complementarity, which may reduce competition for water during drought events. We therefore expected diversity to buffer tree response to drought. Validating these hypotheses would indicate that diversity, through favorable interactions among individuals, may increase the mean and reduce the variance of tree growth. This would demonstrate that interactions among individuals may contribute to the stabilizing effect of diversity in forest ecosystems.

2.4 Material and Methods

The study was conducted in five one ha sites within both temperate and boreal mixed wood stands of Eastern Canada (Fig. S1). Two boreal mixed wood stands (D1823 and D1847) were located in Western Quebec in the balsam fir - white birch bioclimatic domain. The three other sites (ABI, BIC, SUT) laid within temperate mixed wood stands. One site (ABI), was located at the northern limit of the mixed hardwood forest subzone, in the balsam fir - white birch domain. Another site (BIC), was located in St-Lawrence Lowlands, in the balsam fir - yellow birch domain. Finally, the third site (SUT), was located in Eastern Townships, in the sugar maple - basswood domain. The ABI, BIC and SUT sites corresponded to one ha sub plots established within larger sites (of 4, 10.24 and 20 ha, respectively). All sites were mature forests stands

undisturbed by logging, for the exception of the BIC site, which was selectively harvested prior to being designated a national park in 1984. Site altitudes, coordinates and their topographic, climatic and soil characteristics can be found in Aussenac et al (2017).

All trees equal or above 10 cm in diameter at breast height (DBH) were mapped and their DBH were measured in 2011. In 2014, we randomly selected 70 individuals per species and site (when present) in five DBH classes for coring. Sampling intensity was stratified across DBH classes to follow the distribution of each species. Two cores were extracted on the opposite sides of the trunk at breast height for each of the selected trees. Cores were measured at 0.01 mm precision, cross-dated and quality checked following standard dendrochronological methods (Stokes & Smiley 1996).

Species richness on the study sites ranged from five to 14 species yielding a total of 20 species (Fig. S2). We considered cores from six species whose growth were previously shown to be correlated positively to summer precipitation and negatively to summer temperature or summer drought at our study sites (Aussenac *et al.* 2017): eastern white cedar (*Thuja occidentalis L.*), white spruce (*Picea glauca (Moench) Voss*), trembling aspen (*Populus tremuloides Michx.*), balsam fir (*Abies balsamea L.*), red maple (*Acer rubrum L.*), and sugar maple (*Acer saccharum Marshall*).

We limited the radius within which neighbors could interact with focal trees to 20 m. For D1823 and D1847 sites, cores of trees located at less than 20 m from the sites edges were not considered since tree size and position information were not available outside these sites, which prevent proper estimation of interactions among individuals for those trees. All cores were considered for ABI, BIC and SUT sites since trees were measured and mapped outside the one ha sub plots there.

Several insect outbreaks of tent caterpillar (*Malacosoma disstria Hubner.*) occurred during the 1991-2013 period in Eastern Canada (Sutton & Tardif 2009) and caused large reductions in trembling aspen growth, suggesting that trees responded more to defoliation events rather than to climate during these periods. We, therefore, removed periods of tent caterpillar outbreaks from our analyses to avoid bias in our estimation of climate-growth relationships, following the method of Aussenac et al. (2017). We removed from the analyses the cores for which tree rings were impossible to measure due to wood rot. Thus, we had at our disposal 12 to 56 individuals per species and site, yielding a total of 671 individuals (Table S1).

We used the BioSIM 10.3 software (Régnière & St-Amant 2007) to generate site-specific annual series of mean Canadian Drought Code (*DC*) calculated over the June to August period. The *DC* is calculated from daily maximum temperature, 24-hr precipitation and dates of snow cover to estimate the daily rate of soil drying (Lawson & Armitage 2008). It reflects the water content of the deep compact organic layers. For each site, BioSIM interpolated data from the eight closest weather stations using inverse distance weighting, while adjusting for differences in latitude, longitude and elevation between the data and the sites.

2.4.1 Statistical analyses

We estimated diversity around focal trees using the Shannon diversity index (*H*) which measures diversity as a function of species proportion (*pi*) in the community. Here, the focal trees were the cored individuals. For $i = 1,...,s$ species within a radius (r = 20 m) around a focal tree, the Shannon diversity index was given by:

$$H = -\sum_{i=1}^{s} p_i \ln (p_i) \qquad \text{(eqn 2.1)}$$

where $p_i = ba_i/BA$, with ba_i being the basal area of species i in the neighborhood of a focal tree and BA being the total basal area in the neighborhood. We calculated ba_i and BA using a single DBH value for each neighbor, the one measured in 2011, since past DBH could be reconstructed only for focal trees, i.e. cored trees. We, therefore, limited the time window of our analyses to the 1991-2013 period to make sure that neighborhood diversity measured in 2011 reflects the growing conditions of focal trees. In doing so, we assumed changes in neighborhood diversity to be insignificant during the last 20 years (before coring).

Using a mixed model, we measured the effect of diversity on tree growth and on tree response to drought to identify the role of interactions in the diversity-stability relationship. The model describes tree annual basal area increment (BAI) as a function of tree size (DBH), summer drought (DC), diversity (H), and an interaction between diversity and summer drought. We chose to include all species in the same mixed model to have sufficient power to evaluate the interaction between diversity and summer drought. A preliminary power analysis showed that we had not enough individuals per species/site to run specific versions of this model (Table S2).

Species (sp) and sites (si) were considered as random effects. We also considered the composition around focal trees ($compo$) as a random effect, to disentangle the effects of diversity and composition on tree growth. The composition within a radius (r = 20 m) around each focal tree was identified using a vector of 1 and 0 indicating the presence/absence (respectively) of all species on our sites. Because 20 different species are present on our sites, we expected to obtain a large number of compositions, among which some could be underrepresented. This potential lack of replication could artificially inflate the random effects associated to composition and, this way, prevent us from detecting significant fixed effects. To avoid that situation, we only worked

with compositions that appeared at least 4 times in our data, i.e. associated to at least 4 trees (we also worked with compositions associated to at least 10 trees).

We log transformed *BAI* to obtain normally distributed residuals. The model was given by:

$$log(\widehat{BAI_{sp,si,compo}}) = (\alpha_0 + a_{sp} + a_{si} + a_{compo}) + (\beta_1 + b_{1,sp} + b_{1,si})DBH + (\beta_2 + b_{2,sp} + b_{2,si})DC + \beta_3 H + \beta_4 (H.DC) \quad \text{(eqn 2.2)}$$

$$log(BAI_{sp,si,compo}) \sim \mathcal{N}(log(\widehat{BAI_{sp,si,compo}}), \sigma^2) \quad \text{(eqn 2.3)}$$

$$a_{sp,si,compo} \text{ and } b_{sp,si,compo} \sim MV\mathcal{N}(O, \Sigma) \quad \text{(eqn 2.4)}$$

where *DBH, DC*, and *H* are the fixed effects; a_{sp}, a_{si} and a_{compo} are random intercepts accounting for the effect of species, sites and neighborhood compositions on the population intercept; $b_{1,sp}$, $b_{1,si}$ are random slopes accounting for the effect of species and sites on the size-growth relationship; and $b_{2,sp}$, $b_{2,si}$ are random slopes accounting for the effect of species and sites on tree response to drought. Sites random effects are nested in species random effects. We standardized all variables (i.e. we subtracted their mean and divided them by their standard deviation.) in order to compare parameter estimates. The observations $log(BAI_{sp,si,compo})$ were assumed to follow a normal distribution ($\mathcal{N}$) with mean $log(\widehat{BAI_{sp,si,compo}})$ and variance σ^2 (eqn 2.3), and the random parameters were assumed to follow a multivariate normal distribution ($MV\mathcal{N}$) centred on 0 and with Σ the matrix containing the variances and covariances between the random effects (eqn 2.4). We used the the *lmer* function from the R package *lme4* (Bates *et al.* 2017) to fit our model.

Based on our **H2.1** hypothesis, we expected that β_3 would be positive, indicating that diversity may promote tree growth. We also expected that β_4 would be positive,

indicating that diversity may buffer tree response to drought, consistently with our **H2.2** hypothesis.

We computed the credible intervals of mixed model parameters using the 2.5 and 97.5% quantiles of their posterior distribution. Parameters were significant at the 1% level, if 99 % of their posterior distribution were larger or smaller than 0, respectively. We obtained the parameters' posterior distributions using the *sim* function from the R package *arm* (Gelman *et al.* 2016). The *sim* function generated posterior distributions from the joint posterior distribution of the model parameters, using non-informative prior distributions, i.e. it simulated values for each parameter while accounting for the correlation among parameters. We computed the marginal and conditional R^2 (R2m and R2c respectively; Nakagawa & Schielzeth 2013; Johnson 2014), which describe the proportion of variance explained by the fixed effects alone, and the proportion of variance explained by both the fixed and random effects, respectively. R^2_m and R^2_c were calculated with the *r.squaredGLMM* function from the R package *MuMIn* (Bartoń 2016).

2.5 Results

Both versions of the model (considering compositions associated to at least 4 or 10 trees) highlighted the significant effects of tree size, summer drought and diversity on tree growth (Table 1 and S3). Tree size and diversity had a positive effect on tree growth while summer drought had a negative effect. It is worth noting that the effects of drought and diversity are comparable in strength. Besides, diversity buffered tree response to drought.

Random intercepts were variable across species and sites, indicating that species had different intrinsic growth rates modulated by site conditions (e.g. edaphic and climatic

conditions). Random intercepts were also variable across neighborhood compositions indicating that the neighbors' identity also impacted tree growth. Furthermore, random slopes indicated that the size-growth relationship as well as the response to summer drought were variable across species and modulated by site conditions.

The number of focal trees and growth observations included in both versions of the model are presented in Table S4 and S5.

The distribution of the species richness values and the Shannon diversity indices measured in the focal trees' neighborhood are shown in Fig. S3 and S4, respectively.

2.6 Discussion

We found that diversity promoted tree growth and buffered tree response to drought, supporting hypotheses **H2.1** and **H2.2**. These outcomes indicate that diversity, through favorable interactions, may increase the mean and reduce the variance of tree growth. Interactions among individuals may, therefore, contribute to the stabilizing effect of diversity in forest ecosystems. These results are consistent with previous studies showing diversity had a positive effect on tree growth (Potvin & Gotelli 2008; Jucker *et al.* 2014b; Chen *et al.* 2016; Chamagne *et al.* 2017; Fichtner *et al.* 2017) and a buffering effect on tree response to climate (Lebourgeois *et al.* 2013; Pretzsch, Schütze & Uhl 2013; Jucker *et al.* 2014a).

The contribution of interactions among individuals to the stabilizing effect of diversity does not question the stabilizing effect of growth asynchronicity highlighted in previous studies (Jucker *et al.* 2014a; Aussenac *et al.* 2017). Rather, these mechanisms are likely to occur simultaneously. Our results indicate that growth asynchrony may occur among heterospecific trees, as suggested by species-specific responses to

summer drought. These differences we observed in response to summer drought necessarily generate growth asynchrony and thereby stabilize the community-level productivity.

Our results also show that the effect of diversity on growth is large enough to rank among the major drivers of forest productivity, such as climate. This outcome is consistent with previous studies showing that the impacts of species loss on primary productivity are of comparable magnitude to the impacts of drought, ultraviolet radiation, climate warming, ozone, acidification, elevated CO2, herbivory, fire and certain forms of nutrient pollution (Cardinale *et al.* 2012). Diversity should, therefore, be considered in projections of forest productivity under the future climate, and be included as an integral part of climate change research and policy. In contrast, the fact that the effects of drought and diversity are comparable in strength in our analysis deviates from previous findings that tree growth is primarily affected by competition, before climate (Zhang, Huang & He 2015). Interestingly, our results rather emphasize these two factors are interacting to affect tree growth. Besides, the fact that we detected a buffering effect of diversity on tree response to drought in our rather mesic stands suggests diversity may stabilize productivity even in cases where water availability is not a major limiting factor for growth.

Our results show that site conditions (e.g. edaphic and climatic conditions) may impact the stabilizing effect of diversity by affecting the mean and variance of tree growth. Indeed, we found that site conditions affected tree growth (i.e. the intercept of our model and the size-growth relationship) and tree response to summer drought. Climate harshness and soil fertility may drive the effect of site on tree growth while the soil water supply may drive the effect of site on tree response to drought. Site conditions could also impact the stabilizing effect of diversity by modulating interactions among individuals. Indeed, favorable interactions among trees were found to be more frequent

as site conditions become harsher (Paquette & Messier 2011) as predicted by the stress gradient hypothesis (Bertness & Callaway 1994).

The stabilizing effect of diversity may also be modulated by species identity, as evidenced by our finding that composition affected tree growth (i.e. the intercept of our model). This effect of composition may arise from the differences among species in their competitive effect (Canham, LePage & Coates 2004). This result is consistent with previous studies showing that both diversity and composition impact ecosystem productivity (Tilman *et al.* 1997; Hector *et al.* 2011).

Our study helps better understand the mechanisms underlying the diversity-stability relationship. Not only we found that differentiated responses to fluctuating environmental conditions will promote asynchrony and reduce the variability in community productivity, our results show that interactions among individuals will also increase individual growth and buffer their response to climatic fluctuations. To our knowledge, this mechanism has never been documented before, neither theoretically nor empirically. Our work suggests that increasing forest diversity could be a silvicultural strategy allowing to maintain a stable productivity in the face of environmental fluctuations. Further studies are needed to determine whether these conclusions stand across a range of climates and forest types.

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2.9 Tables

Tab. 2.1: Summary of fixed effects and standard deviation (sd) of random effects and residuals for the model considering compositions associated to at least 4 trees. Variables associated with the fixed effects are shown in brackets. The 2.5% and 97.5% quantiles of the posterior distributions were used to define the 95% credible interval of fixed effects. The 50% quantiles indicate the parameters estimates. Parameters were significant if 99% (***) of their posterior distribution were larger or smaller than 0. The model $R^2_m = 0.34$ and $R^2_c = 0.62$.

	2.5%	50%		97.5%	sd
α_0 (intercept)	6.198	6.485	***	6.797	
a_{sp}					0.363
a_{si}					0.195
a_{compo}					0.145
β_1 *(DBH)*	0.390	0.541	***	0.680	
$b_{1,sp}$					0.153
$b_{1,si}$					0.160
β_2 *(DC)*	-0.082	-0.058	***	-0.035	
$b_{2,sp}$					0.023
$b_{2,si}$					0.016
β_3 *(H)*	0.043	0.060	***	0.078	
β_4 *(H.DC)*	0.009	0.022	***	0.034	
residual					0.567

2.11 Supplementary information

Tab. 2.S1: Number of trees cored per species and site.

Tab. 2.S2: Power of the species-specific models to detect the effect of *H.DC*.

Tab. 2.S3: Summary of fixed effects and standard deviation (sd) of random effects and residuals for the model considering compositions associated to at least 10 trees.

Tab. 2.S4: Number of focal trees included in the model considering compositions associated to at least 4 trees.

Tab. 2.S5: Number of focal trees included in the model considering compositions associated to at least 10 trees.

Fig. 2.S1: Location of study sites.

Fig. 2.S2: Basal area of all species present at each site.

Fig. 2.S3: Distribution of the species richness values measured in the focal trees' neighborhood.

Fig. 2.S4: Distribution of the Shannon diversity indices measured in the focal trees' neighborhood.

Tab. 2.S1: Number of trees cored per species and site. Species are coded with their initials: Ab (*Abies balsamea*), Ar (*Acer rubrum*), As (*Acer saccharum*), Pg (*Picea glauca*), Pt (*Populus tremuloides*), To (*Thuja occidentalis*)

	Ab	Ar	As	Pg	Pt	To	*total*
D1823	16			16	18	27	77
D1847	12			20	18	26	76
ABI	50	45	54	44		24	217
BIC	48	47	48		52		195
SUT	50		56				106
total	176	92	158	80	88	77	671

Tab. S2: Power (expressed as a percentage ±95% CI) of the species-specific models to detect the effect of *H.DC*. A power of 80% is traditionally considered as the minimum threshold. No species had enough individuals to detect the effect of *H.DC* with a power greater than 80%. This indicated that the power to reject the null hypothesis of zero trend in *H.DC* was lower than 80%. Site (*si*) and composition (*compo*) were the only random effects considered in these models. Here, we only worked with compositions that appeared at least 4 times in our data, i.e. associated to at least 4 trees. Models are coded with the initials of their associated species: Ab (*Abies balsamea*), Ar (*Acer rubrum*), As (*Acer saccharum*), Pg (*Picea glauca*), Pt (*Populus tremuloides*), To (*Thuja occidentalis*). We used the *powerSim* function from the R package *simr* (Green & MacLeod 2016) to perform power calculations.

models	power (%)
Ab	27.27 (16.14; 40.96)
Ar	16.36 (7.77; 28.80)
As	43.64 (30.30; 57.68)
Pg	23.64 (13.23; 37.02)
Pt	23.64 (13.23;37.02)
To	18.18 (9.08; 30.90

References

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Tab. 2.S3: Summary of fixed effects and standard deviation (sd) of random effects and residuals for the model considering compositions associated to at least 10 trees. Variables associated with the fixed effects are shown in brackets. The 2.5% and 97.5% quantiles of the posterior distributions were used to define the 95% credible interval of fixed effects. The 50% quantiles indicate the parameters estimates. Parameters were significant if 99% (***) of their posterior distribution were larger or smaller than 0. The model $R^2_m = 0.33$ and $R^2_c = 0.61$.

	2.5%	50%		97.5%	sd
α_0 (intercept)	6.144	6.449	***	6.766	
a_{sp}					0.376
a_{si}					0.156
a_{compo}					0.139
β_1 *(DBH)*	0.393	0.528	***	0.667	
$b_{1,sp}$					0.146
$b_{1,si}$					0.154
β_2 *(DC)*	-0.079	-0.054	***	-0.030	
$b_{2,sp}$					0.024
$b_{2,si}$					0.018
β_3 *(H)*	0.047	0.066	***	0.084	
β_4 *(H.DC)*	0.012	0.024	***	0.037	
residual					0.571

Tab. 2.S4: Number of focal trees included in the model considering compositions associated to at least 4 trees. A total of 27 compositions out of 89 were thus considered. The number of growth observations are shown in brackets. Species are coded with their initials: Ab (*Abies balsamea*), Ar (*Acer rubrum*), As (*Acer saccharum*), Pg (*Picea glauca*), Pt (*Populus tremuloides*), To (*Thuja occidentalis*)

	Ab	Ar	As	Pg	Pt	To	*total*
D1823	16 (362)			16 (368)	18 (342)	27 (621)	77 (1693)
D1847	12 (264)			20 (440)	18 (303)	26 (598)	76 (1605)
ABI	48 (1055)	37 (809)	41 (929)	40 (880)		17 (384)	183 (4057)
BIC	38 (873)	34 (782)	35 (772)		40 (754)		147 (3181)
SUT	34 (782)		48 (1087)				82 (1869)
total	148 (3336)	71 (1591)	124 (2788)	76 (1688)	76 (1399)	70 (1603)	565 (12405)

Tab. 2.S5: Number of focal trees included in the model considering compositions associated to at least 10 trees. A total of 20 compositions out of 89 were thus considered. The number of growth observations are shown in brackets. Species are coded with their initials: Ab (*Abies balsamea*), Ar (*Acer rubrum*), As (*Acer saccharum*), Pg (*Picea glauca*), Pt (*Populus tremuloides*), To (*Thuja occidentalis*)

	Ab	Ar	As	Pg	Pt	To	*total*
D1823	16 (362)			16 (368)	18 (342)	27 (621)	77 (1693)
D1847	12 (264)			20 (440)	18 (303)	26 (598)	76 (1605)
ABI	44 (967)	37 (809)	41 (929)	19 (418)		17 (384)	158 (3507)
BIC	38 (873)	34 (782)	35 (772)		40 (754)		147 (3181)
SUT	22 (506)		40 (903)				62 (1409)
total	132 (2972)	71 (1591)	116 (2604)	55 (1226)	76 (1399)	70 (1603)	520 (11395)

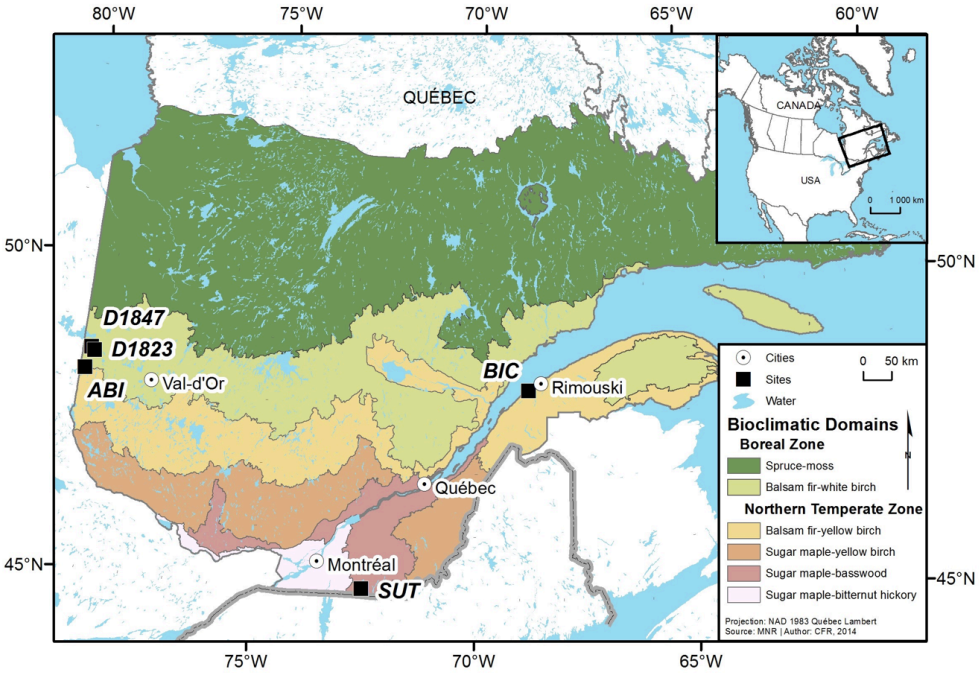

Fig. 2.S1: Location of study sites.

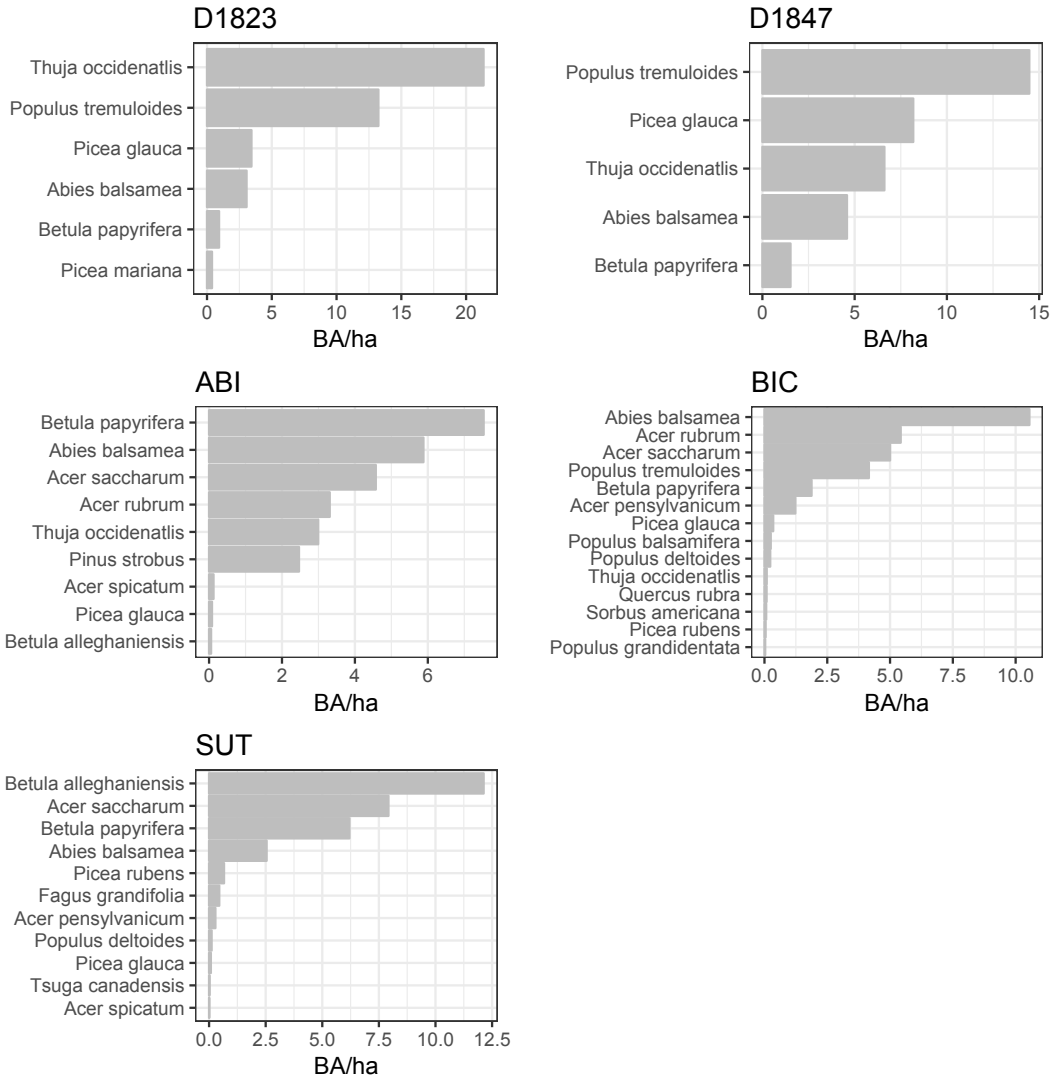

Fig. 2.S2: Basal area of all species present at each site.

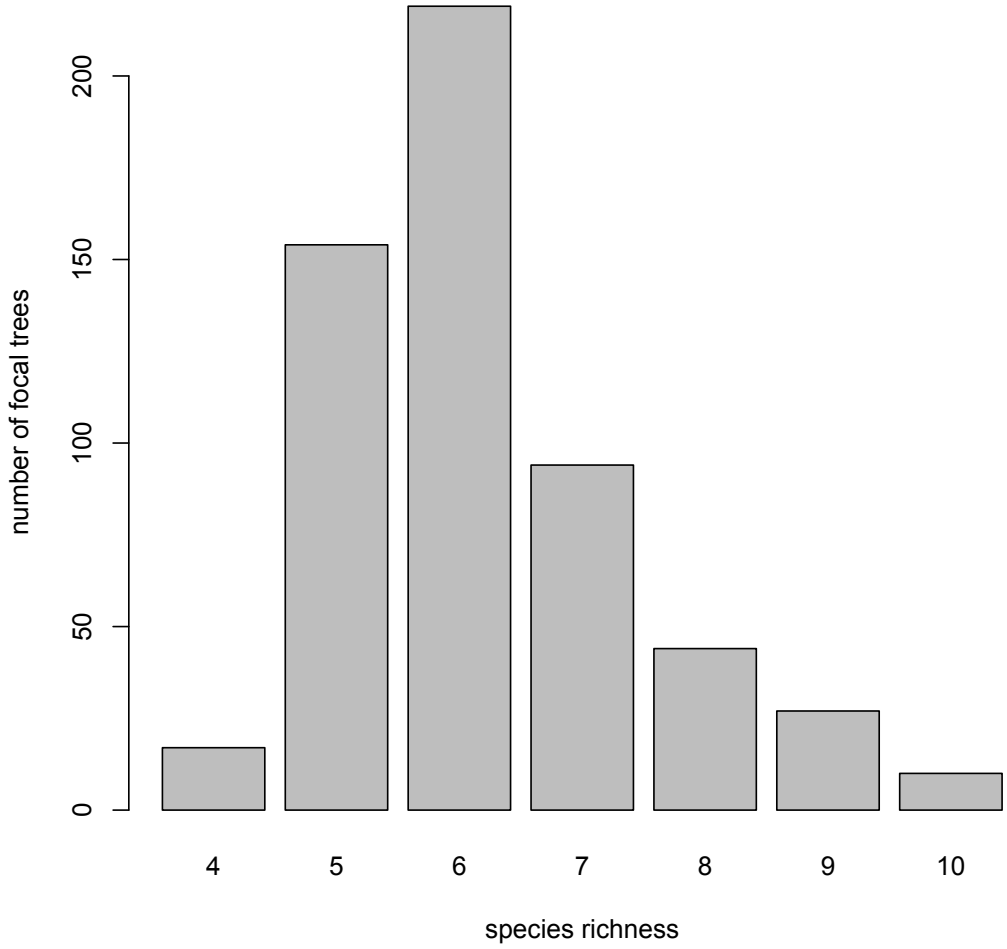

Fig. 2.S3: Distribution of the species richness values measured in the focal trees' neighborhood. Here, the focal trees are those included in the model considering compositions associated to at least 4 trees.

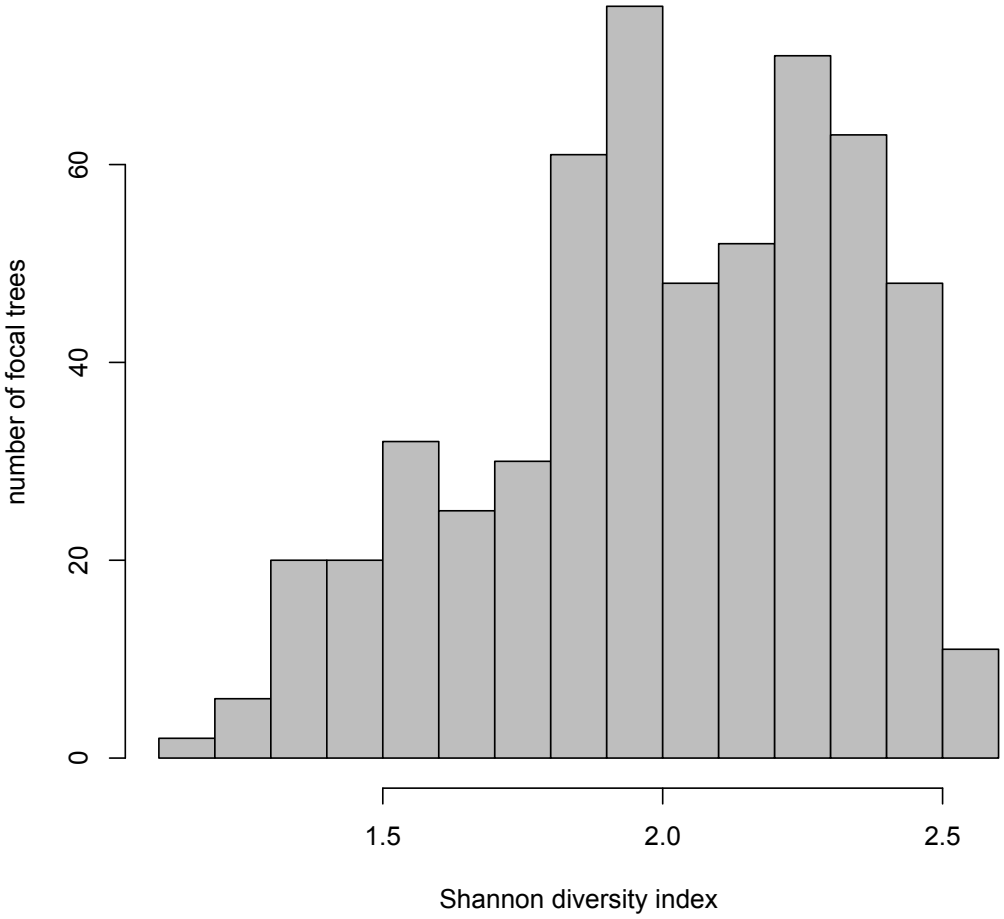

Fig. 2.S4: Distribution of the Shannon diversity indices measured in the focal trees' neighborhood. Here, the focal trees are those included in the model considering compositions associated to at least 4 trees.

CHAPITRE 3 : THE STABILIZING EFFECT OF SPECIES DIVERSITY ON FOREST PRODUCTIVITY UNDER CLIMATE CHANGES

(L'EFFET STABILISANT DE LA DIVERSITÉ DES ESPÈCES SUR LA PRODUCTIVITÉ FORESTIÈRE FACE AUX CHANGEMENTS CLIMATIQUES)

Raphaël Aussenac[1]*, Yves Bergeron[1], Loïc D'Orangeville[2,3], Louis Duchesne[4], Dominique Gravel[5], Daniel Houle[4,6], Igor Drobyshev[1,7]

[1] Chaire industrielle CRSNG-UQAT-UQAM en aménagement forestier durable, Institut de recherche sur les forêts, Université du Québec en Abitibi-Témiscamingue (UQAT), 445 boul. de l'Université, Rouyn-Noranda, Québec, J9X 5E4, Canada; [2] Centre d'Étude de la Forêt, Université du Québec à Montréal, Case Postale 8888, Succursale Centre-Ville, Montreal, Quebec H3C 3P8, Canada; [3] Department of Biology, Indiana University, 1001 East 3rd Street, Jordan Hall 142, Bloomington, IN 47405-7005, United States ; [4] Direction de la Recherche Forestière, Ministère des Forêts, de la Faune et des Parcs du Québec, 2700 Einstein, Québec City, Quebec G1P 3W8, Canada; [5] Chaire de recherche en écologie intégrative, Département de biologie, Faculté des sciences, Université de Sherbrooke, 2500 Boulevard Université, Sherbrooke, Québec, J1K 2R1, Canada; [6] Consortium sur la Climatologie Régionale et l'Adaptation aux Changements Climatiques (Ouranos), 550 Sherbrooke W, Montreal, Quebec H3A 1B9, Canada; [7] Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, P.O. Box 49, 230 53 Alnarp, Sweden

*Auteur correspondant :
Raphaël Aussenac, Chaire industrielle CRSNG-UQAT-UQAM en aménagement forestier durable, Institut de recherche sur les forêts, Université du Québec en Abitibi-Témiscamingue (UQAT), 445 boul. de l'Université, Rouyn-Noranda, Québec, J9X 5E4, Canada. E-mail : raphael.aussenac@uqat.ca

3.1 Abstract

There is mounting evidence that species diversity increases the temporal stability of forest productivity in the face of environmental fluctuations, suggesting it could help mitigate the adverse effects of climate changes. This stabilizing effect of diversity mainly relies on the asynchrony of species response to environmental fluctuations and on favourable interactions among heterospecific trees. However, the diversity-stability relationship in forest ecosystems has never been studied under future climate predictions. Here, we used climate simulations and dendrochronological data to investigate the effect of diversity on forest productivity in the face of inter-annual climatic fluctuations and progressive climatic changes. We found species diversity may stabilise forest productivity in a more variable climate and in the face of progressive climatic changes. However, the stabilizing mechanisms involved in the face of inter-annual climatic fluctuations may be different from those involved in the face of progressive climatic changes. Differences in species-specific responses and favourable interactions among individuals contributed to the stabilizing effect of diversity in the face of inter-annual climatic fluctuations. In contrast, differences in species-specific responses alone contributed to the stabilizing effect of diversity in the face of progressive climatic changes. Our work suggests increasing tree species diversity may stabilize forest productivity in the face of climate changes.

Key words: biodiversity, dendrochronology, growth asynchrony, ecosystem functioning, stability, climate changes, tree growth, pant-climate interactions, plant-plant-interactions

3.2 Résumé

Un nombre croissant d'études suggère que la diversité des espèces augmente la stabilité temporelle de la productivité forestière face aux fluctuations environnementales. La diversité pourrait ainsi limiter les effets néfastes des changements climatiques. Cet effet stabilisant de la diversité repose principalement sur l'asynchronicité de réponse des espèces aux fluctuations environnementales et sur les interactions favorables entre les arbres hétérospécifiques. Toutefois, la relation stabilité-diversité dans les écosystèmes forestiers n'a jamais été étudiée face au climat futur. Ici, nous avons utilisé des simulations climatiques et des données dendrochronologiques pour étudier l'effet de la diversité sur la productivité forestière face aux fluctuations climatiques interannuelles et aux changements climatiques progressifs. Nous avons observé que la diversité des espèces pourrait stabiliser la productivité forestière dans un climat plus variable et face aux changements climatiques progressifs. Cependant, les mécanismes stabilisants impliqués face aux fluctuations climatiques interannuelles pourraient être différents de ceux impliqués face aux changements climatiques progressifs. Les différences de réponse des espèces et les interactions favorables entre individus ont contribué à l'effet stabilisant de la diversité face aux fluctuations climatiques interannuelles. En revanche, seules les différences de réponses des espèces ont contribué à l'effet stabilisant de la diversité face aux changements climatiques progressifs. Notre travail suggère qu'une augmentation de la diversité des espèces pourrait stabiliser la productivité forestière face aux changements climatiques.

Mots clés : biodiversité, dendrochronologie, asynchronicité de croissance, fonctionnement des écosystèmes, stabilité, changements climatiques, croissance des arbres, interactions plante-climat, interactions plante-plante

3.3 Introduction

Climate changes may alter the functioning of forest ecosystems and thereby jeopardize the provision of essential ecosystem services to humanity, in particular, timber production (Boisvenue & Running 2006; Bonan 2008; Allen *et al.* 2010; Lindner *et al.* 2010; Gauthier *et al.* 2015; Charney *et al.* 2016). Increasing tree species diversity has been proposed as a management strategy that could mitigate the adverse effects of climate changes on forest productivity (Jucker *et al.* 2014a; Aussenac *et al.* 2017). Indeed, diversity has been found to stabilize forest productivity under fluctuating climatic conditions, indicating that mixed stands may maintain their total productivity under a wider range of environmental conditions than pure stands. However, whether diversity stabilizes forest productivity under the future climate has never been investigated directly.

Temporal stability (TS, Tilman 1999) has been used to measure the stability of forest productivity. It is measured as the inverse of the coefficient of variation (mean/variance) of the annual productivity of a stand. The mean of the annual productivity of a stand may be decomposed as the sum of the mean annual growth of all individuals in the stand, and its variance - as the sum of the annual growth variances and covariances of all individuals in the stand (Aussenac *et al.* 2017). Any factor affecting one of the three components of *TS* (mean, variance and covariance) may, therefore, impact the *TS* of forest productivity.

The expected increase in the mean annual temperature and in the frequency and intensity of extreme climatic events (Stocker, Dahe & Plattner 2013) may impact the *TS* of forest productivity. Depending on the species and regions considered, warmer temperatures may enhance or reduce tree growth and thereby the *TS* of forest productivity. On the other hand, more frequent extreme climatic events could reduce

the *TS* of forest productivity in three different ways: (1) by increasing the frequency of growth anomalies, and thereby the variance of tree growth (Latte, Lebourgeois & Claessens 2015; Ols *et al.* 2016); (2) by increasing growth synchrony, i.e. covariance among trees (Latte, Lebourgeois & Claessens 2015; Shestakova *et al.* 2016); and (3) by reducing tree mean growth (Lindner *et al.* 2014; Latte, Lebourgeois & Claessens 2015; Ols *et al.* 2016). In addition to these direct effects on tree growth, climate changes may reduce the *TS* of forest productivity by increasing the frequency and intensity of disturbances, such as wildfires, windstorms, or insect outbreaks (Dale *et al.* 2001).

Diversity may stabilize forest productivity under climate changes by impacting the three components of *TS.* Indeed, differences in species-specific responses to climatic fluctuations induce a lower growth covariance among heterospecific trees than among conspecific trees (Jucker *et al.* 2014a; Aussenac *et al.* 2017). This growth asynchrony allows growth compensation among trees, which ultimately stabilize the productivity at the community level. In addition, favourable interactions (i.e. reduced competition and facilitation) among heterospecific trees may enhance stand growth (Potvin & Gotelli 2008; Jucker *et al.* 2014b; Chamagne *et al.* 2017) and buffer tree response to climatic fluctuations, thereby reducing the variance of tree growth (Lebourgeois *et al.* 2013; Pretzsch, Schütze & Uhl 2013; Jucker *et al.* 2014a). Diversity may further increase *TS* through stand level processes. It may increase forest productivity by increasing tree size and tree density, via more efficient canopy packing (Jucker, Bouriaud & Coomes 2015; Pretzsch & Schütze 2016; Williams *et al.* 2017). Finally, it may reduce forest sensitivity to various disturbances such as windstorms (Schütz *et al.* 2006), pathogen invasions (Haas *et al.* 2011), or insect outbreaks (Jactel & Brockerhoff 2007; Castagneyrol *et al.* 2013).

We used climate simulations and tree-ring collections from the Québec Forest Inventory to investigate the effect of diversity on forest productivity under climate

changes. We focused on pure and mixed stands of trembling aspen (*Populus tremuloides Michx.*) and balsam fir (*Abies balsamea L.*). These two species are well suited for this study for several reasons. They are abundant and economically important. Furthermore, they are both sensitive to summer drought (Hogg, Brandt & Kochtubajda 2002; D'Orangeville *et al.* 2013), a climatic event expected to gain prominence in the future in Québec (Ouranos 2015). In addition, aspen and fir may show some growth asynchrony, since tree species typically respond differently to climatic fluctuations. As one species growth decreases, the growth of the other may decrease less sharply or even increase thus compensating the growth decline of the first species. These compensations could stabilize stand productivity in the face of inter-annual climatic fluctuations (e.g. drought event) but also in the face of less abrupt changes (e.g. progressive increase in the mean annual temperature).

We first investigated the effect of diversity on forest productivity in the face of inter-annual climatic fluctuations. For that, we built species-specific mixed models to describe the effect of mixture on tree growth and on tree response to drought, temperature and precipitation, while accounting for the effect of tree size, stand maturity and edaphic conditions. Using climate simulations from four regional and 11 global climate models, we predicted tree growth from 1950 to 2100. Then, we calculated the *TS* of forest productivity over multiple periods of 20 years. These analyses enabled us to identify the effect of diversity in a relatively stable climate (where the mean and the variance of climatic variables are assumed to be constant). We hypothesized (**H3.1**) that diversity increases the stability (*TS*) of forest productivity in the face of inter-annual climatic fluctuations and that this stabilizing effect persists under the future climate. We, therefore, expected mixed stands to be more stable than pure stands. We analysed the effect of diversity on the three components of *TS* to better understand the mechanisms underlying the diversity-stability relationship. Thereafter, we investigated the effect of diversity on forest productivity in the face of progressive

climatic changes. We hypothesized (**H3.2**) that diversity stabilizes forest productivity in the face of progressive climatic changes. To test this hypothesis, we compared aspen and fir simulated growth trends over the 1950-2100 period. We expected species to show some long-term growth asynchrony, enabling long-term growth compensation between species. We also expected species long-term growth trends to be less pronounced in mixed stands than in pure stands, indicating favourable interactions among heterospecific trees buffered species response to progressive climatic changes.

3.4 Material and methods

3.4.1 Study area

We conducted our study in the managed forest of Québec, Canada, from approximately lat. 45° to 50° N and long. 64° to 80° W. The study area extends over two vegetation zones: the northern temperate zone in the south, dominated by deciduous and mixed stands, and the boreal zone in the north, characterized by evergreen coniferous stands. Fire, spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks and harvesting are the main disturbances driving forest dynamics in this area (Girard, Payette & Gagnon 2008), although spruce budworm outbreaks tend to occur south of 48.5° N, in balsam fir forests (Pureswaran *et al.* 2015).

3.4.2 Data collection

We obtained data from the temporary and permanent forest plots of the Québec forest inventory. This inventory is based on a stratified sampling design (MRNF 2009). Aerial photographs were first used to identify stands characteristics (composition, density, height, age), edaphic properties (slope, drainage, deposit), and perturbations. Thereafter, 400 m^2 circular plots were proportionally allocated in each strata according to their respective surface area. These plots describe the managed forests of Québec comprehensively. Within each plot trees equal or above 9 cm in diameter at breast

height (DBH) were identified and measured. Soil texture and moisture regime were also characterized during sampling. In addition, tree cores were collected at one meter aboveground according to a strict sampling protocol. In temporary plots, three trees were cored: one was selected randomly, another was selected randomly among the four biggest trees (in DBH) of the dominant species, and the third had a diameter closest to the mean diameter of the dominant tree species. In permanent plots, up to nine trees were cored: five of which were selected randomly, two were selected randomly among the four biggest trees (in DBH) of the dominant species, one had a diameter closest to the mean diameter of the dominant tree species, and the last had a basal area at breast height closest to the 30^{th} percentile of the distribution of stem basal area for the dominant species. Cores were prepared (dried and sanded) following standard dendrochronological methods (Stokes & Smiley 1996; Speer 2010). Tree ring widths were first identified using binocular, and then measured at 0.001 mm precision using WinDendro software (Regent Instruments, Quebec).

3.4.3 Data selection

For the purpose of this study, we only worked with data from sample plots where the cumulative basal area (BA) of balsam fir and trembling aspen (DBH >= 10 cm) represented at least 90% of the total stand BA. We therefore worked both with mixed and pure stands. Following the approach of D'Orangeville et al. (2016), we adopted an iterative *a posteriori* selection procedure to remove series containing possible measurement errors, because traditional cross-dating would have been extremely time-consuming for such a large dataset. First, we grouped sample plots by landscape unit (median area = 3100km^2), using the Land Hierarchical Classification System (LHCS), which classifies Québec into units similar in climate, vegetation or geomorphology (Ministère des Ressources Naturelles – Secteur des Forêts 2013). Then, we built a master chronology per species for each landscape unit by averaging all individual series in the landscape unit. Finally, we sequentially dropped individual series the least

correlated to the master chronology, rebuilt the master chronology, and repeated this process until all individual series were significantly correlated to the master chronology, and until the master chronology displayed an expressed population signal (EPS) larger than 0.85. We limited our analyses to post-1949 period due to low replication in tree-ring data and inferior climate data quality prior to that date.

Spruce budworm outbreaks occurred every 25 to 40 years in North-Eastern North-America during the 20th century (Morin *et al.* 2009). These outbreaks caused large reductions in balsam fir growth, suggesting that trees responded more to defoliation events than to climate during these periods. We, therefore, calibrated our species-specific models on the 1985-2004 period, to avoid two major defoliation peaks and thus bias in the estimation of climate-growth relationships. Only complete growth series over the 1985-2004 period were retained. Analyses were thus performed on 952 growth series from 380 balsam firs and 572 trembling aspens, yielding a total of 455 sites and 18088 annual growth observations.

3.4.4 Climate

Over the study area, climate ranges from humid temperate in the south, with hot and humid summers and long cold winters, to boreal in the north, with cooler summers and longer, colder winters. Over the 1985-2004 period, annual mean temperatures of sites ranged from 0.13° C to 4.38° C (5th and 95th percentile), and annual total precipitations ranged from 815 mm to 1263 mm (5th and 95th percentile).

3.4.5 Past climatic data

We used the BioSIM 10.3 software (Régnière 1996; Régnière & St-Amant 2007) to generate site-specific annual mean temperatures (T_{an}), annual total precipitation (P_{an}), and daily Canadian Drought Code (DC_d) over the 1985-2004 period. The DC_d is calculated from daily maximum temperature, 24-hr precipitation and dates of snow

cover to estimate the daily rate of soil drying (Lawson & Armitage 2008). It reflects the water content of the deep compact organic layers. For each site, BioSIM interpolated data from the eight closest weather stations using inverse distance weighting, while adjusting for differences in latitude, longitude and elevation between the data and the sites.

3.4.6 Simulated climatic data (1950-2100)

We obtained simulation of T_{an}, P_{an} and DC_d over the 1950-2100 period from a set of four regional and 11 global climate models (RCM and GCM, respectively). For the DC_d calculation, we set the dates of the snow-free period from April 1 to October 31. Climate simulations were driven using two different greenhouse gas emissions scenarios used in the IPCC fifth Assessment Report (Stocker, Dahe & Plattner 2013) and referred as Representative Concentration Pathways (RCPs; Moss *et al.* 2010): RCP8.5 and RCP4.5. The RCP8.5 assumes greenhouse emissions will continuously rise throughout the 21st century, while the RCP4.5 assumes emissions will reach a peak around 2040. We, therefore, worked with 30 different climate simulations, which enabled us to take into account uncertainty in future climate simulations. An increase of 4.65°C in the average T_{an} of our sites is projected, from 2.52°C during the 1985-2004 period to 7.17°C during the 2081-2100 period. An increase of 13% (129.33 mm) in the average P_{an} of our sites is also projected, from 984.17 mm during the 1985-2004 period to 1113.51 during the 2081-2100 period.

3.4.7 Edaphic conditions

The majority of sites (76.3%) are characterized by a xeric to mesic soil moisture regime, the remaining sites (23.7%) being characterized by a hygric soil moisture regime. Medium and fine-textured mineral soil deposits were found on most sites (41.5% and 40% respectively). Coarse-textured mineral soil deposits were less frequently encountered (18.5%).

3.4.8 Growth Models

We built species-specific mixed models to describe the effect of mixture on tree basal area increment (BAI) and on tree response to drought, temperature and precipitation, while accounting for the effect of tree size, stand maturity (measured as the stand total BA - BA_t) and edaphic conditions. Mixed models allowed us to account for the temporal and spatial autocorrelation in our data due the non-independency of growth measurements from the same individual, and from individuals on the same site. We described the effect of mixture on tree growth using two variables: species proportion in the stand (Pr, expressed as a percentage of BA_t) and competition. We estimated competition by measuring the net effect of neighbouring trees on the growth of target trees as a function of the sum of the neighbours' BA. The target trees were those with growth data available, i.e. cored trees. Given the small size of the sample plots (400 m^2), all trees were potential neighbours. However, we only considered neighbours larger than the target tree, since these are more likely to affect the growth of target trees (Huang *et al.* 2013; Ford *et al.* 2016). We calculated C_s and C_h for softwood and hardwood neighbours to take into account the differences in their competitive effect, respectively. We used the maximum value of DC_d on the June to August period, which represents the maximum level of drought reached in the deep compact organic layers, as a measure of drought. We considered the effect of drought both for the year concurrent with and preceding tree growth (DC_m and DC_{mp} respectively). We log transformed BAI to obtain normally distributed residuals and we standardized the variables to make comparable their effects in the model. We, therefore, included 35 fixed effects in our models, among which the effect of:

- Eight continuous variables: DBH +Pr + C_h + C_s + DC_m + DC_{mp} + T_{an} + P_{an}
- two categorical variables: D (the soil drainage, i.e. the soil moisture regime) + T (the soil texture)

- 25 interactions describing the effect of
  - tree size on tree response to drought: $DBH.DC_m + DBH.DC_{mp}$
  - species proportion on tree response to drought: $Pr.DC_m + Pr.DC_{mp}$
  - stand maturity on tree response to species proportion: $Pr.BA_t$
  - competition on tree response to drought: $C_h.DC_m + C_h.DC_{mp} + C_s.DC_m + C_s.DC_{mp}$
  - edaphic conditions on tree response to climate: $T.DC_m + T.DC_{mp} + T.T_{an} + T.P_{an} + D.DC_m + D.DC_{mp} + D.T_{an} + D.P_{an}$
  - edaphic conditions on tree response to competition: $T.C_h + T.C_s + D.C_h + D.C_s$
  - edaphic conditions on tree response to species proportion: T.Pr + D.Pr
  - edaphic conditions on tree response to tree size: T.DBH + D.DBH

We also included random effects for three variables (DBH, DC_m, DC_{mp}) in a nested structure ("individual" nested in "plot"). These random effects enabled us to account for the differences in the tree size effect and in the response to drought among individuals, and among plots. We did not include random effects for T_{an} and P_{an}, since trees usually do not respond to annual variation in T_{an} and P_{an}. Trees rather respond to annual variation in the temperature and precipitation of the growth season. Here, T_{an} and P_{an} are used to describe the effect of the spatial variation of temperature and precipitation on tree growth over the study area. Models were fitted with the *lmer* function from the R package *lme4* (Bates *et al.* 2017).

3.4.9 Variable selection

We used a stepwise procedure to select meaningful variables based on their variance inflation factor (VIF). The VIF measures the proportion of variance in one predictor explained by all the other predictors in the model. While increasingly higher values of VIF indicate increasing multicollinearity, a VIF = 1 indicate no multicollinearity.

Following the approach of Zuur at al. (2010), we sequentially dropped the predictor with the highest VIF, recalculated the VIFs and repeated this process until all VIFs were smaller than 2. This procedure avoided model overfitting and inflation of the parameters' standard errors due to predictors multicollinearity.

3.4.10 Model interpretation

We computed the parameters' credible intervals using the 2.5 and 97.5% quantiles of their posterior distribution. Parameters were significant at the 10, 5 or 1% level, if 90, 95 or 99 % of their posterior distribution were larger or smaller than 0, respectively. We obtained the parameters' posterior distributions using the *sim* function from the R package *arm* (Gelman *et al.* 2016). The *sim* function generated posterior distributions from the joint posterior distribution of the model parameters, using non-informative prior distributions, i.e. it simulated values for each parameter while taking the correlation between the parameters into account. We used the marginal and conditional R^2 (R2m and R2c respectively; Nakagawa & Schielzeth 2013; Johnson 2014), to describe the proportion of variance explained by the fixed factors alone, and the proportion of variance explained by both the fixed and random factors, respectively. R^2_m and R^2_c were calculated with the *r.squaredGLMM* function from the R package *MuMin* (Bartoń 2016).

3.4.11 Growth prediction

We used the simulated climatic data to predict tree growth on the 1950-2100 period. For each tree and each climate simulation, we simulated 10 growth series using different values for the growth models' parameters, randomly drawn from their posterior distribution, and taking into account the residual variation. This enabled us to capture the uncertainty of our growth models in predictions. We, therefore, obtained 300 simulated growth series for each tree, corresponding to the 30 different climate simulations we had (four RCM and 11 GCM driven by two RCPs) multiplied by ten

simulations. We only considered the fixed variation in these simulations. We first predicted tree growth by holding all variables included in the models constant over time, with the exception of climatic variables (T_{an}, P_{an}, DC_m, DC_{mp}). We attributed to trees the diameter they had in 2004. This enabled us to analyse the effect of climate on growth keeping everything else constant. We compared predictions obtained after assigning the same soil texture and drainage to all sample plots to investigate the effect of soil on tree response to climate. We used the *predictInterval* function from the R package *merTools* (Knowles & Frederick 2016) to perform these predictions.

3.4.12 Effect of diversity in the face of inter-annual climatic fluctuations

We investigated the effect of species mixture on the *TS* of forest growth. Diversity has a stabilizing effect if the *TS* measured in a mixed stand is higher than expected from the mean and the variance of the total growth of its constituent species in pure stands weighted by their proportions in the mixed stand. We defined pure stands as stands where one species represented at least 75% of the total stand *BA*. Mixed stands were defined as stands where all species represented less than 75% of the total stand *BA*. Because we had numerous mixed stands having different species proportions, we adopted an approach allowing to compare the *TS* of mixed and pure stands on a complete mixture gradient (from 100% aspen to 100% fir). For that, we first calculated $E[TS_{pure}]$, the expected *TS* of simulated stands of fir and aspen from the mean and the variance of the total growth of both species in pure stands, for all possible combinations of species proportions. Following the same procedure, we calculated $E[TS_{mixed}]$ from the mean and the variance of the total growth of both species in mixed stands. Unlike $E[TS_{pure}]$, $E[TS_{mixed}]$ takes into account interactions among heterospecific individuals, since it was calculated from mixed stands. We calculated $E[TS_{pure}]$ and $E[TS_{mixed}]$ as following (see demonstration in Supplementary Information):

$$E[TS] = \frac{E[\mu]}{E[\sigma]} = \frac{\frac{p_{fir}}{nb_{fir}}\mu_{fir} + \frac{p_{aspen}}{nb_{aspen}}\mu_{aspen}}{\left(\frac{p_{fir}}{nb_{fir}}\right)^2 \sigma_{fir} + \left(\frac{p_{aspen}}{nb_{aspen}}\right)^2 \sigma_{aspen} + 2\frac{p_{fir}\ p_{aspen}}{nb_{fir}nb_{aspen}} cov(fir,aspen)} \qquad \text{(eqn 3.1)}$$

where $E[TS]$ is alternately $E[TS_{pure}]$ or $E[TS_{mixed}]$; $E[\mu]$ is alternately $E[\mu_{pure}]$ or $E[\mu_{mixed}]$ the expected mean growth of a stand calculated from the total growth of both species in pure or mixed stands, respectively; $E[\sigma]$ is alternately $E[\sigma_{pure}]$ or $E[\sigma_{mixed}]$ the expected growth variance of a stand calculated from the total growth of both species in pure or mixed stands, respectively; μ_{fir} and μ_{aspen} - the mean of fir and aspen total growth; σ_{fir} and σ_{aspen} - the variance of fir and aspen total growth; *cov(fir, aspen)* – the covariance of fir and aspen total growth; p_{fir} and p_{aspen} - the species proportions (expressed as a percentage of the stand total *BA*), ranging from 0 to 1 in increments of 0.01, with $p_{fir} + p_{aspen} = 1$; and nb_{fir} and nb_{aspen} the number of plots on which μ_{fir} and σ_{fir}, on one side, and μ_{aspen} and σ_{aspen}, on the other side, were calculated, to take into account the fact that we did not have the same number of pure fir stands and pure aspen stands. We calculated 300 $E[TS]$ values for each combination of p_{fir} and p_{aspen}, corresponding to the 300 different chronologies predicted for fir and aspen total growth. We used the 150 predicted total growth chronologies for each species and climate scenario to build $E[TS]$ envelopes for each scenario. Envelopes corresponded to the complete range of $E[TS]$ values obtained for each combination of species proportions.

To test whether diversity increases the *TS* of forest productivity in the face of inter-annual climatic fluctuations and whether this stabilizing effect persists under the future climate (**H3.1**), we compared $E[TS_{pure}]$ and $E[TS_{mixed}]$ values over the 1985-2004 and the 2081-2100 periods. We expected $E[TS_{mixed}]$ to be greater than $E[TS_{pure}]$ for both periods.

Thereafter, we analysed the effect of diversity on the three components of *TS* to better understand the mechanisms driving the diversity-stability relationship. We sought to determine the effect of species mixture on tree growth by comparing $E[\mu_{pure}]$ and $E[\mu_{mixed}]$ values. We expected $E[\mu_{mixed}]$ to be greater than $E[\mu_{pure}]$ indicating diversity increases tree growth via favourable interactions among heterospecific individuals. Similarly, we investigated the effect of species mixture on the variance of stand growth by comparing $E[\sigma_{pure}]$ or $E[\sigma_{mixed}]$. We expected $E[\sigma_{mixed}]$ to be lower than $E[\sigma_{pure}]$ indicating diversity buffers species response to climate, i.e. reduces species growth variability, via favourable interactions among heterospecific individuals. Finally, we compared $E[TS_{pure}]$ values obtained for mixed stands (p_{fir} and p_{aspen} <1) to those obtained for pure stands (p_{fir} or p_{aspen} = 1) to identify the effect of species growth asynchrony on stand growth *TS*. We expected $E[TS_{pure}]$ values to be greater in mixed stands than in pure stands due to species growth asynchrony. Indeed, since $E[TS_{pure}]$ was calculated from pure stands, it doesn't take into account interactions among heterospecific individuals. The stabilizing effect of mixture expected would, therefore, be the result of species growth asynchrony alone. Thus, the difference between $E[TS_{pure}]$and $E[TS_{mixed}]$ corresponds to the stabilizing effect due to favourable interactions among individuals. We performed theses analyses over the 1985-2004 and the 2081-2100 periods. We also ran these analyses after having assigned the same soil texture and drainage to all sample plots to identify the effect of soil on the diversity-*TS* relationship.

3.4.13 Effect of diversity in the face of progressive climatic changes

We investigated the long-term growth trends of pure and mixed stands over the entire study area, as well as the long-term growth trends of each species in each stand type. We obtained the long-term growth trends of pure fir stands, pure aspen stands and mixed stands by summing separately simulated growth series from these stand types. We obtained species-specific growth chronologies both for pure and mixed stands by

summing separately the simulated growth series from each species in each stand type. We summed the simulated tree growth series according to the climate scenario, the climate model and the simulation of the growth model that generated them. We, therefore, obtained 300 growth chronologies corresponding to different predictions of the total growth of all individuals. We used the 150 predicted growth chronologies corresponding to the 15 climate models multiplied by the ten simulations of the growth model to build growth predictions envelopes for each scenario. External envelopes corresponded to the complete range of predictions, while internal envelopes corresponded to the confidence interval of predictions, calculated using Wilcoxon test. To test whether diversity stabilizes forest productivity in the face of progressive climatic changes (**H3.2**), we compared the growth trends between mixed stands and pure stands. We expected species to show some long-term asynchrony of growth, allowing for long-term growth compensation between species. We also expected species long-term growth trends to be less pronounced in mixed stands than in pure stands as a result of the favourable interactions among heterospecific trees. We studied the effect of soil in these analyses comparing the growth predictions obtained after assigning the same soil texture and drainage to all sample plots.

3.5 Results

After variable selection, our models showed significant effects of tree size, competition, annual temperature, annual precipitation and summer drought on tree growth. These effects depended on soil drainage and texture. Furthermore, tree size and competition appeared to modulate tree response to drought.

3.5.1 Fir growth model

Annual temperature had a positive effect on fir growth on medium-textured soils (Figure 3.1). Annual precipitation could have simultaneously various effects on fir

growth depending on soil drainage and texture: it had a negative effect on growth on all drainage types (xeric, mesic and hygric) and simultaneously a positive effect on growth on medium and fine-textured soils. Both hardwood and softwood competition had a negative effect on fir growth on medium and fine-textured soils while they had no effect on coarse-textured soils. Drought concurrent and preceding tree growth had a negative effect on fir growth for the largest trees and for trees experiencing strong softwood competition. On the other hand, it had a positive effect on the smallest trees and trees experiencing little softwood competition.

3.5.2 Aspen growth model

Annual precipitation had a negative effect on aspen growth on all sites (Figure 3.1). Annual temperature could have simultaneously various effects on aspen growth depending on soil drainage and texture: it had a positive effect on growth on all drainage types (xeric, mesic and hygric) and simultaneously a positive effect on coarse and medium-textured soils or a negative effect on fine-textured soils. Both hardwood and softwood competition had a negative effect on aspen growth on medium and fine-textured soils while they had no effect on coarse-textured soils. Drought concurrent with tree growth had a negative effect on aspen growth on medium and fine-textured soils while they had no effect on coarse-textured soils. Drought preceding tree growth had a negative effect on aspen growth on fine-textured soils while it had no effect on coarse and medium-textured soils. The negative effect of drought preceding tree growth was stronger for the largest trees. Proportion of aspen in the stand had a positive effect on aspen growth in the most mature stands (having the largest total BA) while it had a negative effect in less developed stands.

3.5.3 Random effects

The standard deviation of random effects (Table 3.1) indicated that tree growth was highly dependent on sites and individuals, for both species. The effect of tree size on

growth was particularly dependant on sites and individuals. In comparison, tree response to drought remains relatively similar from one tree to another and from one plot to another.

3.5.4 Effect of diversity in the face of inter-annual climatic fluctuations

We found $E[TS_{mixed}]$ was overall higher than $E[TS_{pure}]$ (Figure 3.2). This outcome indicated that species mixture had a stabilizing effect on stand growth and that favourable interactions among heterospecific individuals contributed to this effect. We also found $E[TS_{pure}]$ was greater for mixed stands ($0 <$ proportion of fir <1) than for pure stands (proportion of fir = 0 or 1) indicating that species growth asynchrony also contributed to this stabilizing effect. The multimodal aspect of the expected *TS* envelopes arose from divergences between climate simulations. The expected mean growth predicted from species growth in pure stands ($E[\mu_{pure}]$) was higher than the expected mean growth predicted from species growth in mixed stands ($E[\mu_{mixed}]$; Figure 3.3). This indicated that species mixture reduced tree growth. Finally, the expected growth variance predicted from species growth in mixed stands ($E[\sigma_{mixed}]$) was lower than the one predicted from species growth in pure stands ($E[\sigma_{pure}]$; Figure 3.4). This indicated that species mixture reduced the variance of species growth, i.e. buffered species response to inter-annual climatic fluctuations through favourable interactions among heterospecific individuals (see chapter 2). These outcomes were persistent regardless of the climate scenario, the period and the soil type considered, although the stabilizing effect of diversity appeared stronger on coarse and medium-textured soils characterized by xeric to mesic moisture regime (Supplementary Information Figure 3.S1, 3.S2 and 3.S3).

3.5.5 Effect of diversity in the face of progressive climatic changes

Aspen and fir had opposite long-term growth trends on all soil types, except on medium-textured soils characterized by a xeric to mesic moisture regime, where both

species growth are expected to increase (Figure 3.5). A slight increase in productivity could be expected in most stands since medium-textured soils characterized by a xeric to mesic moisture regime cover most Québec's forested area. On coarse-textured soils, fir growth is expected to decline while aspen growth is expected to increase. On medium-textured soils characterized by a hygric moisture regime, aspen growth is expected to decrease while fir growth is expected to increase. Finally, on fine-textured soils, aspen growth is expected to decrease while fir growth may remain constant.

These trends were identical in both mixed and pure stands (Figure 3.6 and 3.S4) suggesting favourable interactions among heterospecific trees did not buffer species responses to progressive increases in temperature and precipitation.

3.6 Discussion

Our results showed that diversity may stabilise forest productivity in a more variable climate and in the face of progressive climatic changes, supporting the **H3.1** and **H3.2** hypotheses. However, the stabilizing mechanisms involved in the face of inter-annual climatic fluctuations may be different from those involved in the face of progressive climatic changes.

3.6.1 Stabilizing effect of diversity in the face of inter-annual climatic fluctuations

The observed positive diversity-*TS* relationship stemmed from (i) the differences in species-specific responses to inter-annual climatic fluctuations which enabled inter-annual growth compensation among species, and (ii) the favourable interactions among heterospecific trees which buffered tree responses to inter-annual climatic fluctuations. The positive diversity-*TS* relationship persisted in the future suggesting diversity could stabilize forest productivity in a more variable climate.

The stabilizing effect of diversity in the face of inter-annual climatic fluctuations was stronger on the coarsest textured and driest sites. This may be explained by the fact that both hardwood and softwood competition had a negative effect on growth on medium and fine-textured soils, while they had no effect on coarse-textured soils. These outcomes are consistent with the stress gradient hypothesis which predicts that the relative frequency of facilitation and competition varies inversely across stress gradient, with facilitation being more common under harsh abiotic conditions (Bertness & Callaway 1994).

We found tree growth was lower in mixed stands than in pure stands. This is contrary to previous studies which have shown that diversity may increase tree growth through favourable interactions among heterospecific trees (Potvin & Gotelli 2008; Paquette & Messier 2011; Jucker *et al.* 2014b; Liang *et al.* 2016; Chamagne *et al.* 2017). Our result may be explained by the fact that we worked on a narrow gradient of species diversity (from one to two species). A positive effect of diversity on tree growth could be more easily detected on broader gradients. This result does not mean, however, that diversity reduces stand growth. Indeed, despite its negative effect on tree growth, diversity may increase stand growth by increasing tree density, via more efficient canopy packing (Jucker, Bouriaud & Coomes 2015; Pretzsch & Schütze 2016; Williams *et al.* 2017). However, we could not detect the positive effect of diversity on stand growth due to a more efficient canopy packing since not all trees were cored on the sample plots. Thus, whether mixing aspen and fir reduces or increases stand growth remains to be clarified.

3.6.2 Stabilizing effect of diversity in the face of progressive climatic changes

The stabilizing effect of diversity in the face of progressive climatic changes stemmed from the differences in species-specific responses to these changes which enabled long-term growth compensation among species. On the other hand, favourable interactions had no effect on tree responses to progressive climatic changes, and therefore, did not

contributed to the stabilizing effect of diversity in the face of progressive climatic changes.

The long-term increase in aspen and fir growth predicted by our models on different soil types stems from the increase in annual temperature. This positive impact of warming on tree growth has already been reported in boreal and temperate forests of North-America, especially in regions where water is not a limiting factor (Boisvenue & Running 2006; Huang *et al.* 2010; Lapointe-Garant *et al.* 2010). On the other hand, the decline in aspen growth predicted by our models (essentially on fine-textured soils) stems from the increase in the frequency and intensity of summer droughts, which also corroborates previous predictions made in the same region (Lapointe-Garant *et al.* 2010). The origin of the decline in fir growth on coarse-textured soils is unclear. It may emerge from interactions between different environmental factors rather than from a single factor. However, the observed declines in growth are relatively weak.

3.6.3 Model interpretation

We found that drought had a more detrimental impact on large trees' growth than on small trees' growth. Drought could even increase small trees' growth. These outcomes are consistent with a previous study showing larger trees suffer most during drought in forests worldwide (Bennett *et al.* 2015). The higher sensitivity of large trees to droughts may arise from their inherent vulnerability to hydraulic stress, since they must lift water to a greater height. It may also arise from the higher solar radiation and evaporative demand experienced by their exposed crowns. On the other hand, smaller trees in the understorey face weaker solar radiations, lower temperature and lower wind speed. They may also benefit from release from competition with large trees for nutrients and water, and thus exhibit higher growth rates during droughts. The positive effect of drought on tree growth we found for small trees could also emerge from the fact that water availability is not a major limiting factor for growth in our study area

(D'Orangeville *et al.* 2016). The negative effect of annual precipitation on tree growth we observed for both species on most sites strengthens this hypothesis. This abundance of water may explain why drought had no effect on tree growth on some sites.

We also found that drought had a negative effect on fir trees experiencing strong softwood competition and a positive effect on those experiencing little softwood competition. This counterintuitive outcome may also arise from the abundance of water in our study area. Competition, at low levels, may promote tree growth by drying soils saturated with water. In contrast, water may become a limiting factor at high levels of competition.

Finally, we found aspen growth was positively affected by aspen proportion in the most mature stands while it was negatively affected in the less developed stands. In young stands, aspen could benefit from the reduced competition due to the presence of more fir and less aspen. In contrast, in mature stands, the abundance of fir may negatively affect aspen growth because of the decrease in fertility generated by fir litter over time (Cavard *et al.* 2011).

3.6.4 Conclusion

Our work constitutes a first exploration of the diversity-stability relationship under climate changes in forest ecosystems. We found that increasing tree species diversity could help stabilise forest productivity in a more variable climate and in the face of progressive climatic changes. Our work also suggests that the stabilizing mechanisms may be different depending on the type of climatic changes forest is facing. We obtained these results on a narrow gradient of diversity (from one to two species), suggesting shifting practices away from monoculture to mixed stands constituted of two species could already bring benefits in terms of stability. A transformation of pure stands into mixed stands could be given priority at sites where abiotic conditions are

the harshest, since facilitation is more common there and competition weaker. Our study calls for further analyses to determine whether this increase in stability is accompanied by a decrease in productivity.

3.7 Acknowledgements

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3.9 Tables

Tab. 3.1: Goodness of fit and standard deviation of the nested random effects and the residuals of the species-specific growth models.

	standard deviation	
	fir	aspen
Individual		
intercept	0.47497	0.286302
DBH	0.45505	0.184794
DC_m	0.01642	0.011257
DC_{mp}	0.01935	0.008867
Plot		
intercept	0.24480	0.367786
DBH	0.59918	0.432006
DC_m	0.03117	0.072465
DC_{mp}	0.02857	0.063722
residuals	0.21969	0.356662
R^2_m	0.25	0.19
R^2_c	0.96	0.82

3.10 Figures

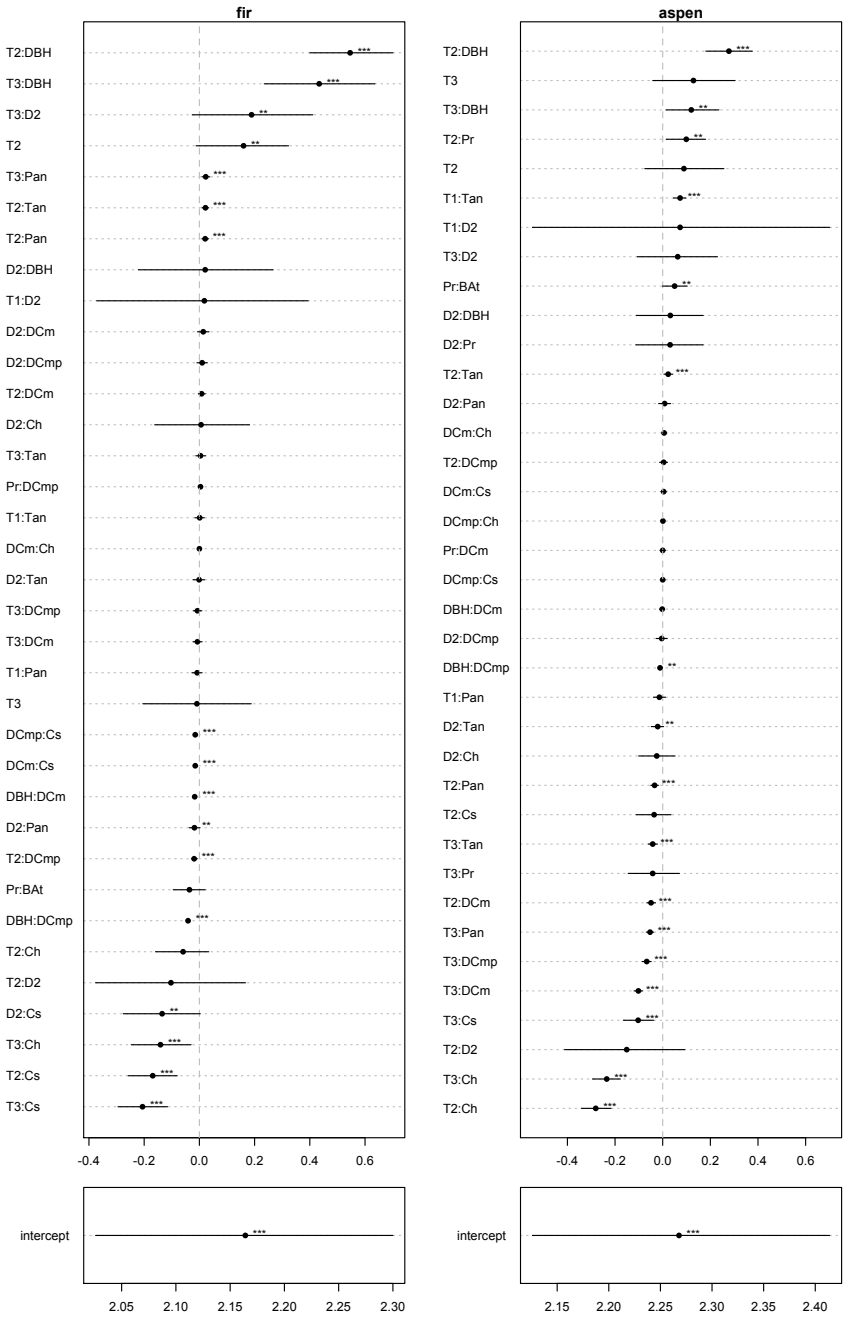

Fig. 3.1: Parameters of the species-specific growth models after variable selection. Parameters are presented on the vertical axes for both the balsam fir (left) and the trembling aspen (right) growth models. The horizontal axes represent the parameters' strength. Dots indicate the parameters' estimate and segments indicate the parameters' credible intervals.

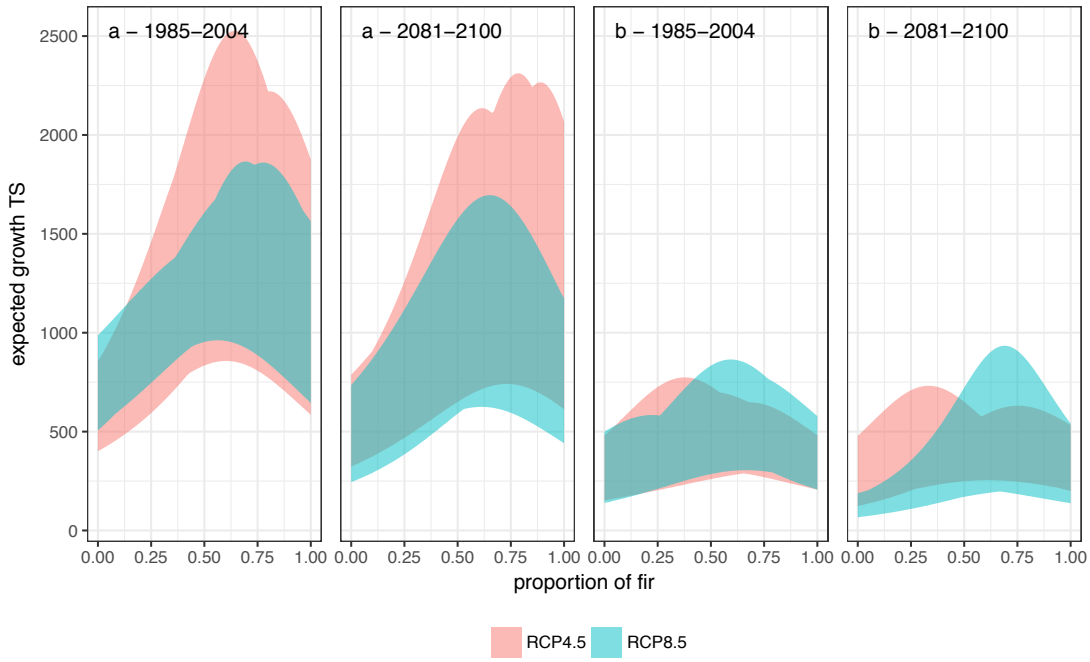

Fig. 3.2: Expected *TS* of mixed stands. Expected *TS* of mixed stands calculated from species growth in mixed stands ($E[TS_{mixed}]$; **a**) and in pure stands ($E[TS_{pure}]$; **b**) over the 1985-2004 and the 2081-2100 periods and under each climate scenario (RCP4.5 and RCP8.5). The proportion of aspen is 1 – proportion of fir.

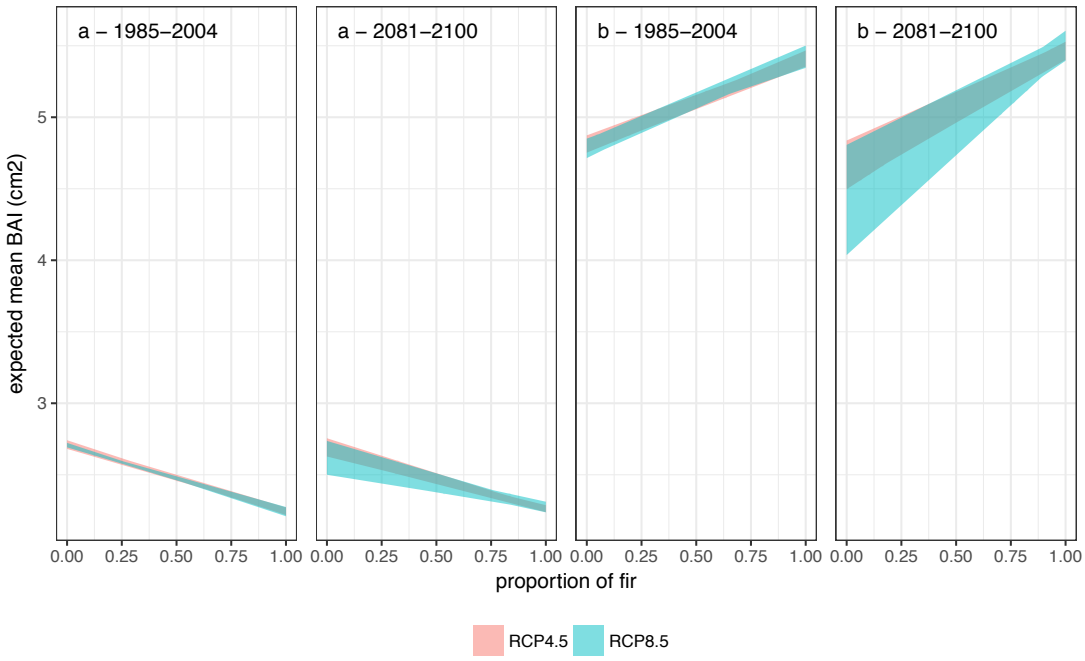

Fig. 3.3: Expected mean growth of mixed stands. Expected mean growth of mixed stands calculated from species growth in mixed stands ($E[\mu_{mixed}]$; **a**) and in pure stands ($E[\mu_{pure}]$; **b**) over the 1985-2004 and the 2081-2100 periods and under each climate scenario (RCP4.5 and RCP8.5). The proportion of aspen is 1 – proportion of fir.

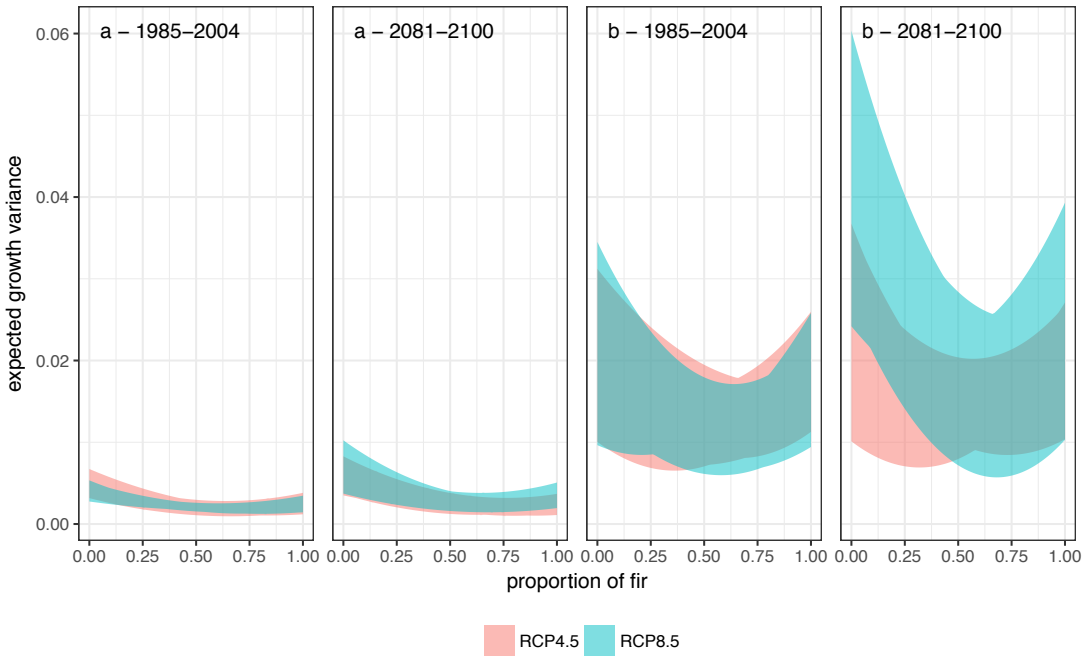

Fig. 3.4: Expected growth variance of mixed stands. Expected growth variance of mixed stands calculated from species growth in mixed stands ($E[\sigma_{mixed}]$; **a**) and in pure stands ($E[\sigma_{pure}]$; **b**) over the 1985-2004 and the 2081-2100 periods and under each climate scenario (RCP4.5 and RCP8.5). The proportion of aspen is 1 – proportion of fir.

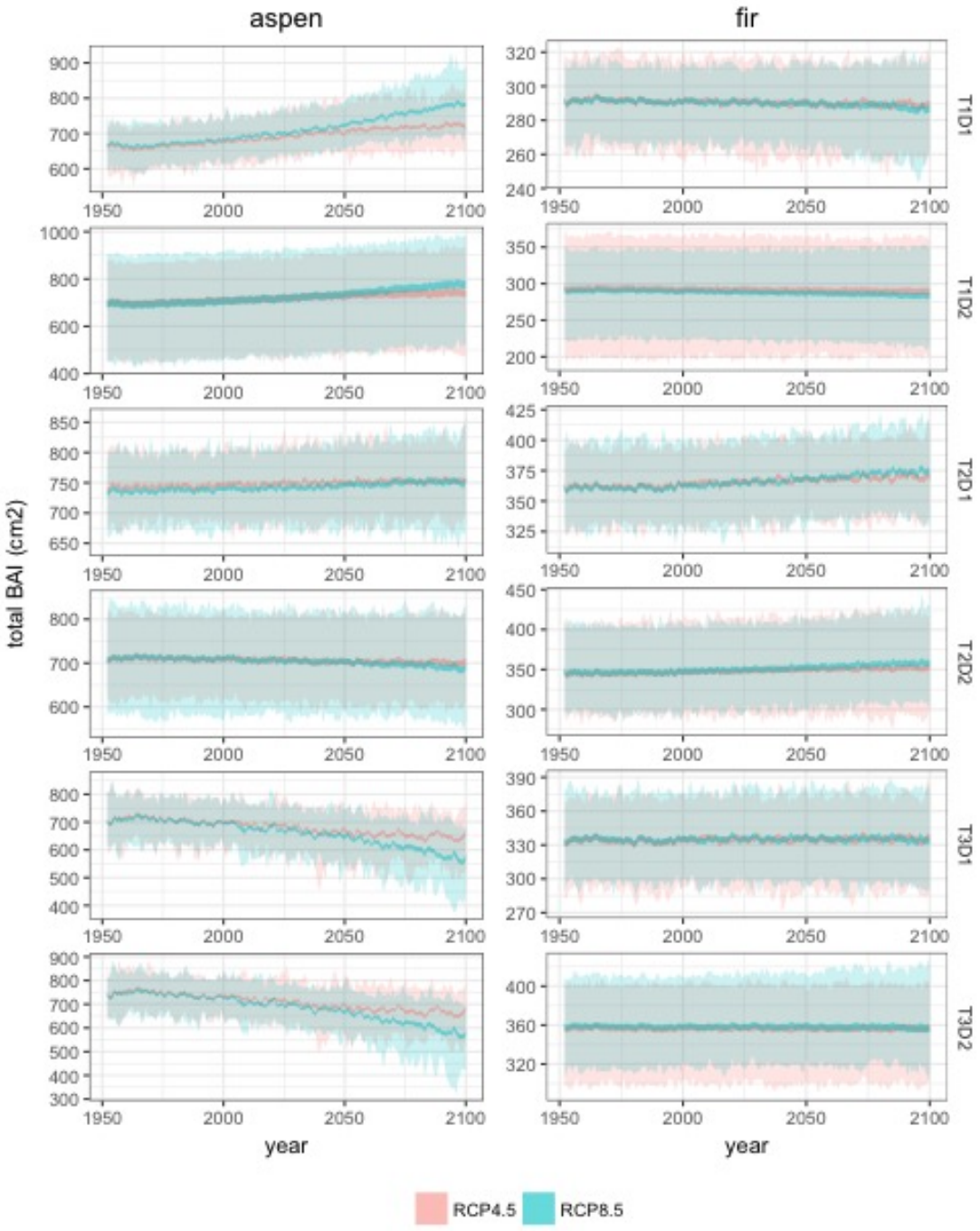

Fig. 3.5: Growth of aspen and fir in different soil types, over the 1950-2100 period and under each climate scenario (RCP4.5, RCP8.5). **T1**, **T2** and **T3** correspond to coarse, medium and fine-textured soils respectively. **D1** and **D2** correspond to xeric-mesic and hygric moisture regime respectively.

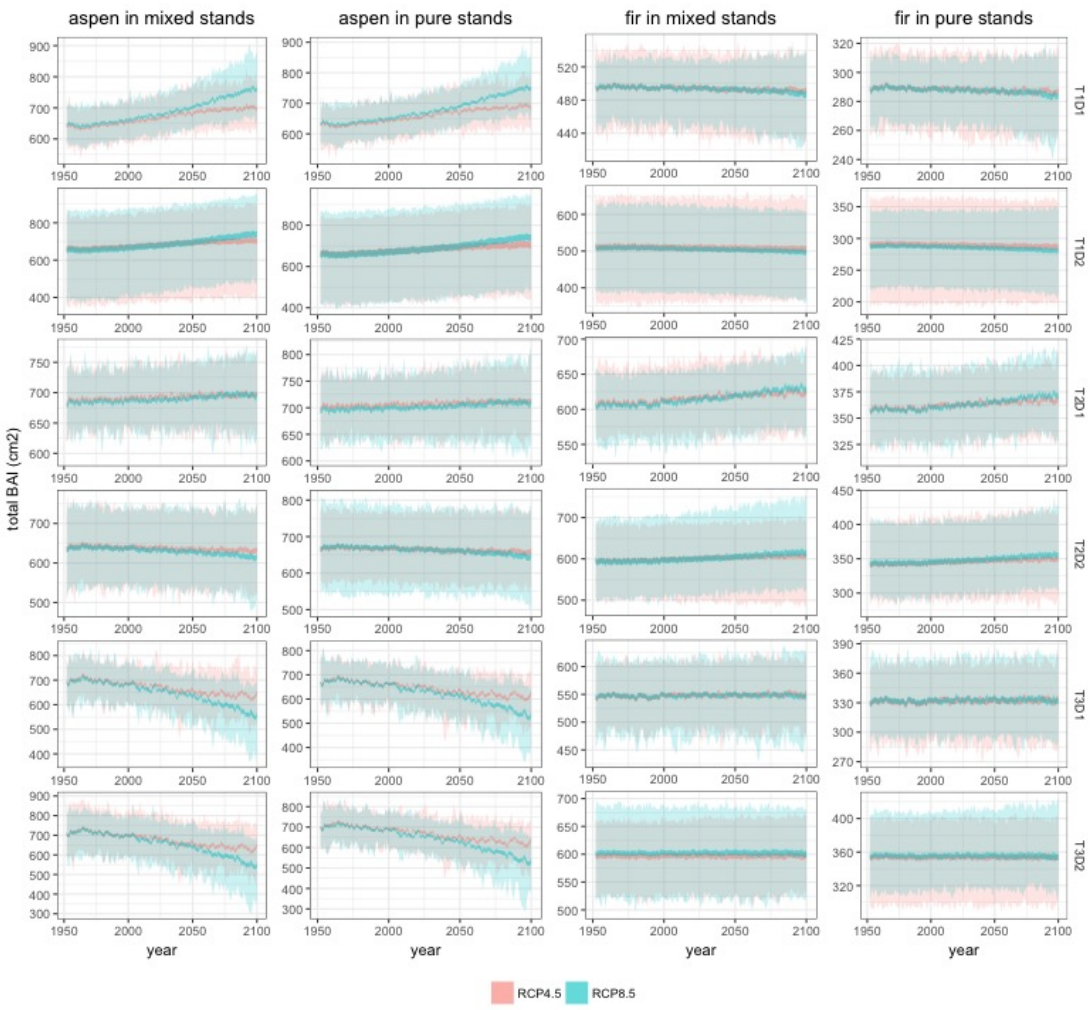

Fig. 3.6: Growth of aspen and fir in mixed and pure stands, in different soil types, over the 1950-2100 period and under each climate scenario (RCP4.5, RCP8.5). **T1**, **T2** and **T3** correspond to coarse, medium and fine-textured soils respectively. **D1** and **D2** correspond to xeric-mesic and hygric moisture regime respectively.

3.11 Supplementary information

Demonstration 3.S1: Temporal stability of a mixed stand calculated from the mean and the variance of the total growth of its constituent species in pure stands weighted by their proportion.

Fig. 3.S1: Expected *TS* of mixed stands calculated on each soil type

Fig. 3.S2: Expected mean growth of mixed stands calculated on each soil type.

Fig. 3.S3: Expected growth variance of mixed stands calculated on each soil type.

Fig. 3.S4: Growth difference between mixed and pure stands for aspen and fir on each soil type.

Demonstration 3.S1: Temporal stability of a mixed stand calculated from the mean and the variance of the total growth of its constituent species in pure stands weighted by their proportions.

The variance of a weighted sum of variables may be expressed as:

$$\sigma\left(\sum_{i=1}^{i=n} p_i X_i\right) = \sum_{i=1}^{i=n}\sum_{j=1}^{j=n} p_i p_j cov(X_i, X_j)$$

were p_i and p_j are the weights of the X_i and X_j variables

and for $X_i = X_j$, $cov(X_i, X_j) = \sigma(X_i) = \sigma(X_j)$. Then,

$$\sigma\left(\sum_{i=1}^{i=n} p_i X_i\right) = \sum_{i=1}^{i=n} p_i^2 \sigma(X_i) + 2\sum_{i=1}^{i=n}\sum_{j>i}^{j=n} p_i p_j cov(X_i, X_j)$$

Therefore, the productivity variance of a mixed stand of fir and aspen may be calculated from the variance of the productivity of both species in pure stands, weighted by species proportion as following:

$$\sigma = p_{fir}^2 \sigma_{fir} + p_{aspen}^2 \sigma_{aspen} + 2 p_{fir} p_{aspen} cov(fir, aspen)$$

The mean of a weighted sum of variables may be expressed as:

$$\mu = \sum_{i=1}^{i=n} p_i X_i$$

Therefore, the mean productivity of a mixed stand of fir and aspen may be calculated from the mean productivity of both species in pure stands, weighted by species proportion as following:

$$\mu = p_{fir}\, \mu_{fir} + p_{aspen}\, \mu_{aspen}$$

Thus, the TS of the productivity of a mixed stand of fir and aspen may be calculated from the mean and the variance of the total growth of its constituent species in pure stands weighted by their proportion:

$$TS = \frac{\mu}{\sigma} = \frac{p_{fir}\mu_{fir} + p_{aspen}\mu_{aspen}}{p_{fir}^2 \sigma_{fir} + p_{aspen}^2 \sigma_{aspen} + 2 p_{fir} p_{aspen} cov(fir, aspen)}$$

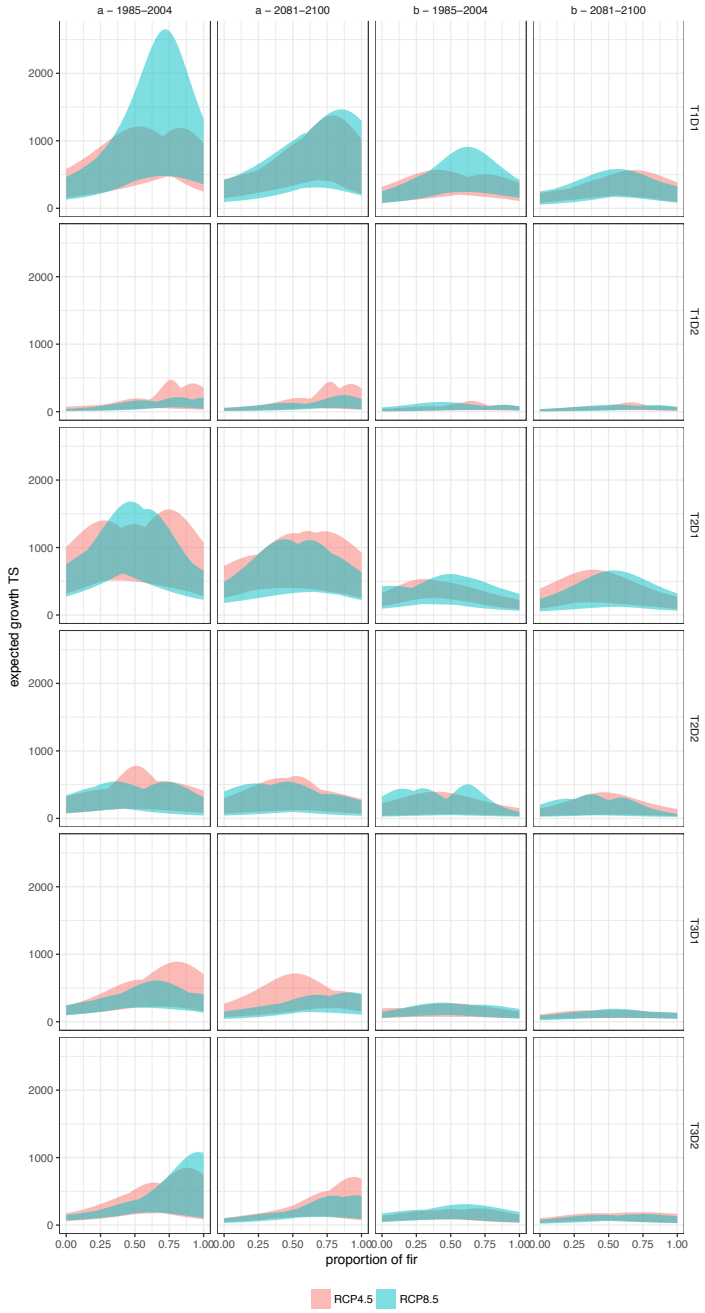

Fig. 3.S1: Expected *TS* of mixed stands calculated on each soil type Expected *TS* of mixed stands calculated on each soil type from species growth in mixed stands ($E[TS_{mixed}]$; **a**) and in pure stands ($E[TS_{pure}]$; **b**) over the 1985-2004 and the 2081-2100 periods and under each climate scenario (RCP4.5 and RCP8.5). **T1**, **T2** and **T3** correspond to coarse, medium and fine-textured soils respectively. **D1** and **D2** correspond to xeric-mesic and hygric moisture regime respectively.

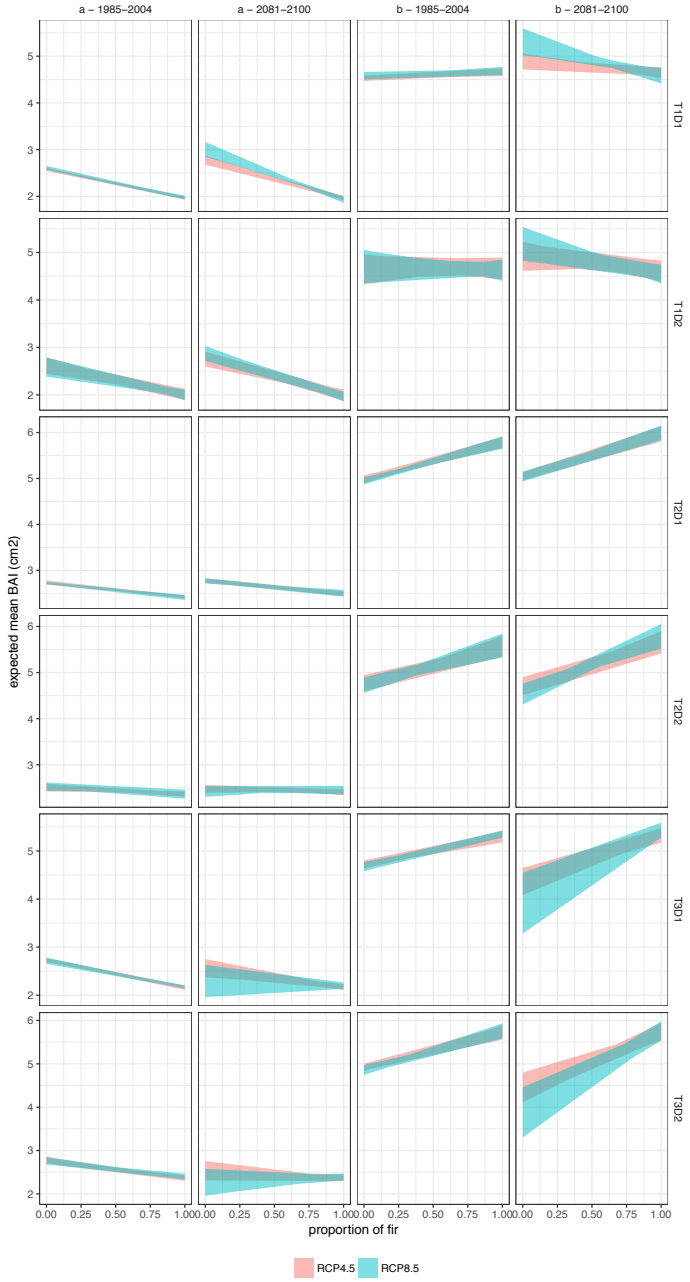

Fig. 3.S2: Expected mean growth of mixed stands calculated on each soil type. Expected mean growth of mixed stands calculated on each soil type from species growth in mixed stands ($E[\mu_{mixed}]$; **a**) and in pure stands ($E[\mu_{pure}]$; **b**) over the 1985-2004 and the 2081-2100 periods and under each climate scenario (RCP4.5 and RCP8.5). **T1**, **T2** and **T3** correspond to coarse, medium and fine-textured soils respectively. **D1** and **D2** correspond to xeric-mesic and hygric moisture regime respectively.

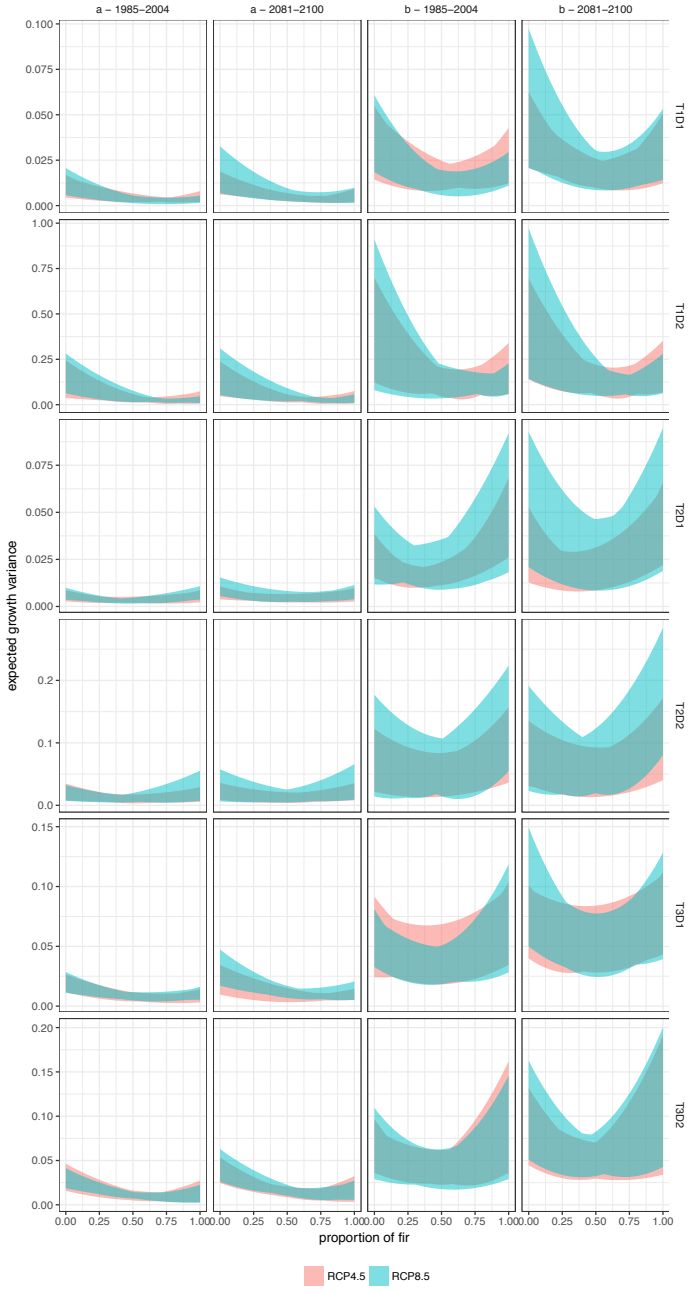

Fig. 3.S3: Expected growth variance of mixed stands calculated on each soil type. Expected growth variance of mixed stands calculated on each soil type from species growth in mixed stands ($E[\sigma_{mixed}]$; **a**) and in pure stands ($E[\sigma_{pure}]$; **b**) over the 1985-2004 and the 2081-2100 periods and under each climate scenario (RCP4.5 and RCP8.5). **T1**, **T2** and **T3** correspond to coarse, medium and fine-textured soils respectively. **D1** and **D2** correspond to xeric-mesic and hygric moisture regime respectively.

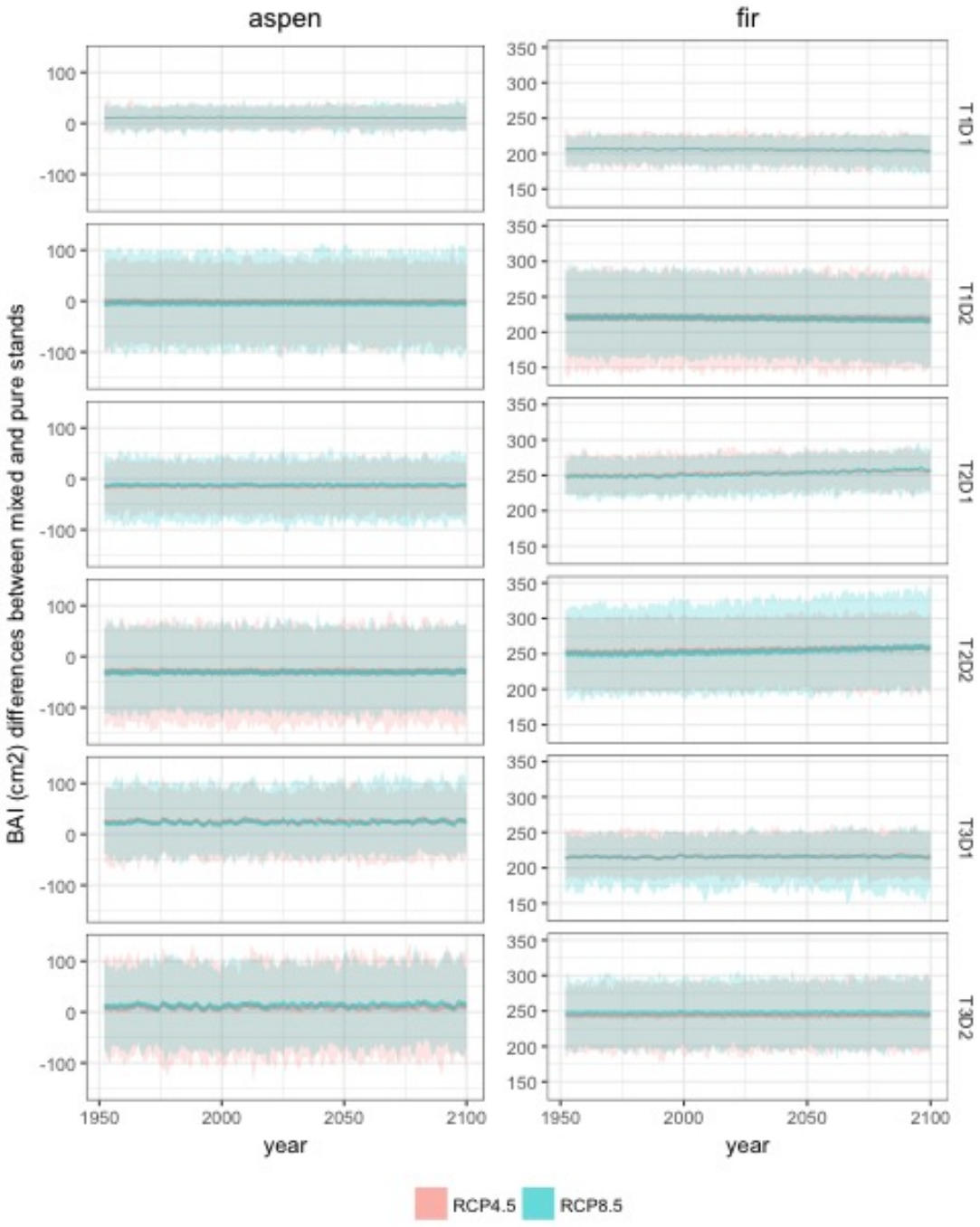

Fig. 3.S4: Growth difference between mixed and pure stands for aspen and fir on each soil type. **T1**, **T2** and **T3** correspond to coarse, medium and fine-textured soils respectively. **D1** and **D2** correspond to xeric-mesic and hygric moisture regime respectively

CONCLUSION GÉNÉRALE

4.1 Rappel des objectifs des chapitres, synthèse et discussion

4.1.1 Chapitre 1

Le premier chapitre de cette thèse avait pour objectif d'identifier l'effet de la richesse spécifique sur la stabilité de croissance des forêts. Il s'agissait également de déterminer le rôle de l'asynchronicité de croissance entre individus dans la relation diversité-stabilité. Enfin, nous avons cherché à déterminer si la variabilité intraspécifique de réponse aux fluctuations environnementales jouait un rôle dans la relation diversité-stabilité. Pour cela nous avons adopté une approche par paires d'individus en utilisant des données dendrochronologiques provenant de cinq peuplements forestiers mixtes au Québec. Nous avons mesuré la stabilité temporelle, la moyenne et la variance de la croissance totale de paires d'individus conspécifiques et hétérospécifiques. Nous avons également mesuré la covariance de croissance des individus constituant ces paires. Nous avons travaillé dans des communautés où les populations étaient maintenues constantes afin d'éliminer les effets confondants liés aux dynamiques de populations (*effet de sélection* et *dynamiques compensatoires)*.

Nous avons montré que la diversité tendait à stabiliser la croissance totale des paires d'individus. Ce résultat suggère que la diversité pourrait stabiliser la croissance des forêts face aux fluctuations environnementales, conformément à l'hypothèse H1.1. Ce résultat est donc en accord avec les études précédentes montrant une relation positive

entre diversité et stabilité dans les écosystèmes forestiers (Jucker *et al.* 2014a; Morin *et al.* 2014). Cet effet stabilisant de la diversité provenait, au moins partiellement, d'une plus forte asynchronicité de croissance entre individus hétérospécifiques qu'entre individus conspécifiques, conformément à l'hypothèse H1.2. Jucker *et al.* (2014a) ont mis en évidence ce même mécanisme en étudiant l'effet stabilisant de la diversité en l'absence de dynamiques de populations. Nous avons montré que cette asynchronicité de croissance provenait des différences de réponses des individus aux fluctuations climatiques et aux épidémies d'insectes (livrée des forêts et tordeuse des bourgeons de l'épinette), conformément à l'hypothèse H1.3. Ainsi, nous avons démontré que la variabilité intraspécifique de réponses aux fluctuations environnementales peut moduler l'effet stabilisant de la diversité, conformément aux propositions de de Mazancourt *et al.* (2013). Nous en avons conclu que les mécanismes à l'origine de cette variabilité intraspécifique de réponses pourraient jouer un rôle dans l'effet stabilisant de la diversité. Il pourrait s'agir de l'hétérogénéité spatiale des conditions environnementales (au sein des peuplements) ou des interactions entre individus.

L'effet stabilisant de la diversité était plus fort lorsque les analyses intégraient les épidémies d'insectes en plus des fluctuations climatiques annuelles. Cela s'explique par une augmentation de l'asynchronicité de croissance des individus due à leur sensibilité différentielle à la livrée des forêts et à la tordeuse des bourgeons de l'épinette. La diversité pourrait stabiliser encore d'avantage la croissance des forêts face aux épidémies d'insectes, notamment en augmentant l'abondance des ennemis naturels des insectes phytophages (Cappuccino *et al.* 1998), et en dissimulant les arbres hôtes parmi les non hôtes, ce qui limite l'herbivorie. Ce dernier mécanisme est appelé *effet de dilution des hôtes* (Jactel & Brockerhoff 2007; Castagneyrol *et al.* 2013). Toutefois, une plus grande diversité dans le voisinage des arbres hôtes n'a pas semblé réduire l'impact négatif des insectes. Ce résultat inattendu pourrait s'expliquer par le fait que nous avons calculé la diversité dans le voisinage directe des arbres hôtes. Or, étant donnée la capacité de dispersion importante de la livrée des forêts et de la tordeuse

des bourgeons de l'épinette (Greenbank 1957), les dommages que ces dernières infligent aux arbres pourraient dépendre davantage de la diversité à l'échelle du peuplement ou du paysage. Nos résultats suggèrent donc que certains mécanismes stabilisant pourraient dépendre de la diversité à différentes échelles spatiales. L'intégration des épidémies d'insectes dans nos analyses constitue, par ailleurs, une première étape vers l'étude de la relation diversité-stabilité dans des communautés forestières multitrophiques.

Nous avons observé un effet négatif de la diversité sur la croissance des paires d'individus. Ce résultat semble contraire aux études précédentes montrant un effet positif de la diversité sur la croissance des arbres (Potvin & Gotelli 2008; Paquette & Messier 2011; Jucker *et al.* 2014b; Chamagne *et al.* 2017). Toutefois, ce résultat pourrait être dû au fait que les paires d'espèces étaient constituées d'individus de toutes les tailles. Or, généralement, la croissance radiale initiale augmente avec la taille des arbres puis diminue chez les arbres plus grands. Ainsi, comparer la croissance totale d'une paire de sapins de tailles intermédiaires (en croissance rapide) à une paire composée d'un sapin et d'un bouleau, tous deux de petite taille (en croissance lente), conduirait à la conclusion que la diversité a un effet négatif sur la croissance, alors qu'il s'agirait d'un effet de la taille. La large gamme de tailles d'arbres dans nos données ne permet donc pas de conclure quant à l'effet de la diversité sur la croissance totale des paires d'individus. Par ailleurs, malgré un effet négatif sur la croissance individuelle, la diversité pourrait toute de même augmenter la productivité des peuplements en augmentant la densité des arbres via une meilleure imbrication des houppiers (Jucker, Bouriaud & Coomes 2015; Pretzsch & Schütze 2016; Williams *et al.* 2017). La diversité pourrait donc affecter différemment la croissance selon le niveau d'organisation écologique considéré.

4.1.2 Chapitre 2

Dans le deuxième chapitre de cette thèse, il s'agissait de déterminer si les interactions entre individus jouaient un rôle dans l'effet stabilisant de la diversité sur la croissance des forêts en l'absence de dynamiques de populations, comme suggéré dans le chapitre 1. Pour cela nous avons mesuré l'effet de la diversité sur (i) la croissance des arbres et (ii) leur réponse à la sécheresse en utilisant les mêmes données que dans le chapitre 1.

Nous avons observé que la diversité favorisait la croissance des arbres et tamponnait la réponse des arbres à la sécheresse, conformément aux hypothèse H2.1 et H2.2. Ces résultats indiquent que la diversité, grâce aux interactions favorables entre arbres, peut augmenter la moyenne et réduire la variance de la croissance des arbres, ce qui pourrait ultimement augmenter la stabilité de la productivité forestière. Nos résultats montrent donc que les interactions entre individus peuvent contribuer à stabiliser la productivité des forêts en l'absence de dynamiques de populations. Ils rejoignent les résultats de Jucker *et al.* (2014a) qui ont montré que la relation diversité-stabilité en forêt reposait en partie sur l'effet positif de la diversité sur la croissance individuelle et son effet négatif sur la variabilité de la croissance individuelle. Enfin, nos résultats sont en accord avec les études précédentes montrant un effet positif de la diversité sur la croissance des arbres (Potvin & Gotelli 2008; Paquette & Messier 2011; Jucker *et al.* 2014b; Chamagne *et al.* 2017), ainsi qu'avec les études montrant un effet tampon de la diversité sur la réponse des arbres au climat (Lebourgeois *et al.* 2013; Pretzsch, Schütze & Uhl 2013; Jucker *et al.* 2014a).

Nos résultats montrent également que la diversité pourrait figurer parmi les principaux facteurs contrôlant de la productivité forestière, tels que le climat. Ce résultat est cohérent avec les études antérieures montrant que les impacts de la perte d'espèces sur la productivité primaire sont comparables aux impacts de la sécheresse, des rayons ultraviolets, du réchauffement climatique, de l'ozone, de l'acidification, du CO2 élevé,

des herbivores, du feu et de certaines forme de pollutions (Cardinale *et al.* 2012). La diversité devrait donc être prise en compte dans les projections de productivité forestière dans le climat futur.

Le fait que les effets de la sécheresse et de la diversité soient comparables en magnitude dans notre analyse dévie quelque peu des résultats d'études antérieures suggérant que la croissance des arbres est avant tout affectée par la compétition, puis, dans une moindre mesure, par le climat (Zhang, Huang & He 2015). Nos résultats suggèrent plutôt que ces deux facteurs interagissent pour affecter la croissance des arbres.

Nos travaux suggèrent que l'augmentation de la diversité forestière pourrait être une stratégie sylvicole permettant de maintenir une productivité stable face aux fluctuations environnementales. Toutefois, d'autres études sont nécessaires afin de déterminer si ces conclusions s'appliquent à tous les types de climats et de forêts.

4.1.3 Chapitre 3

Le troisième chapitre de cette thèse avait pour objectif de déterminer si la diversité stabilise la croissance des forêts face aux changements climatiques. Il s'agissait également d'identifier les mécanismes à l'origine de cet effet stabilisant. Pour cela, nous nous sommes intéressés aux peuplements purs et mixtes de peuplier faux-tremble et de sapin baumier au Québec. Nous avons construit un modèle de croissance décrivant l'effet du mélange des espèces sur la croissance des arbres et sur leur réponse à la sécheresse, à la température et aux précipitations. Puis, à l'aide de modèles climatiques, nous avons simulé la croissance des arbres de 1950 à 2100. Dans ce chapitre, tout comme dans les deux précédents, les analyses ont été menées de manière à éliminer les dynamiques de populations afin de mieux identifier les mécanismes à l'origine de la relation diversité-stabilité.

Nos résultats suggèrent que la diversité pourrait stabiliser la croissance des forêts dans un climat plus variable et face aux changements climatiques progressifs, conformément aux hypothèses H3.1 et H3.2. Cependant, les mécanismes de stabilisation impliqués face aux fluctuations climatiques interannuelles pourraient être différents de ceux impliqués face aux changements climatiques progressifs. Face aux fluctuations climatiques interannuelles, les différences de réponse des espèces ainsi que les interactions favorables entre individus hétérospécifiques semblent contribuer à l'effet stabilisant observé. Les différences de réponse des espèces permettent des compensations de croissance entre les espèces. Les interactions favorables, elles, tamponnent la réponse des arbres aux fluctuations climatiques interannuelles. En revanche, les interactions favorables ne semblent pas tamponner la réponse des arbres aux changements climatiques progressifs. Ainsi, face à de tels changements, seules les différences de réponse des espèces semblent contribuer à l'effet stabilisant de la diversité sur la croissance des peuplements.

Toutefois, les interactions entre individus pourraient jouer un rôle dans la relation diversité-stabilité face aux changements climatiques progressifs si l'on considérait les dynamiques de populations. En effet, face à des changements climatiques progressifs, qui par définition se déroulent sur de longues périodes, les mécanismes qui gouvernent la relation diversité-stabilité sont susceptibles d'impliquer les dynamiques de populations. Il pourrait s'agir de *l'effet de sélection* ou de *dynamiques compensatoires*. Ces mécanismes, contrôlés par les interactions entre individus, pourraient avoir un effet stabilisant sur les forêts, à la fois en diminuant la variance de leur productivité et en augmentant leur productivité moyenne (Morin *et al.* 2014; Tobner *et al.* 2016). En revanche, sur de courtes périodes, relativement à la durée de vie des arbres, les dynamiques de populations peuvent être considérées comme nulles. Ainsi, face aux fluctuations climatiques interannuelles les dynamiques de populations sont peu susceptibles de jouer un rôle dans la relation diversité-stabilité.

Nous avons observé que l'effet stabilisant de la diversité face aux fluctuations climatiques interannuelles était plus fort dans les peuplements confrontés à des conditions édaphiques défavorables (sols secs à textures grossières). Cela pourrait provenir du fait que sur ces sols, la compétition entre individus semblait réduite. Ces observations sont compatible avec *l'hypothèse du gradient de stress* qui prédit que la fréquence relative de la facilitation et de la compétition varie inversement le long d'un gradient de stress, la facilitation étant plus fréquente dans des conditions abiotiques difficiles (Bertness & Callaway 1994).

Nous avons également constaté que la proportion de peuplier tendait à augmenter la croissance de ce dernier dans les peuplements les plus matures alors qu'elle tendait à réduire sa croissance dans les peuplements moins développés. Dans les jeunes peuplements, le peuplier pourrait bénéficier d'une compétition réduite lorsque les sapins sont abondants. En revanche, dans les peuplements matures, l'abondance du sapin pourrait affecter négativement la croissance du peuplier en raison de la diminution de la fertilité générée par la litière du sapin au fil du temps (Cavard *et al.* 2011). La diversité pourrait donc affecter la stabilité des forêts en modifiant les conditions édaphiques.

Nous avons également observé que la croissance des individus semblait plus faible dans les peuplements mixtes que dans les peuplements purs. Ce résultat semble contraire aux études précédentes montrant un effet positif de la diversité sur la croissance des arbres (Potvin & Gotelli 2008; Paquette & Messier 2011; Jucker *et al.* 2014b; Chamagne *et al.* 2017). Il pourrait être dû au fait que nous avons travaillé sur un gradient de diversité très étroit (une à deux espèces). Un effet positif de la diversité pourrait être plus facile à détecter sur un gradient de diversité plus large. Tout comme dans le chapitre 1, on ne peut pour autant conclure que la diversité a un effet négatif sur la productivité des forêts. En effet, la diversité pourrait augmenter la productivité

des peuplements en augmentant la densité des arbres via une meilleure imbrication des houppiers (Jucker, Bouriaud & Coomes 2015; Pretzsch & Schütze 2016; Williams *et al.* 2017).

4.2 Synthèse transversale des résultats

Les trois chapitres de cette thèse mettent en évidence un effet stabilisant de la diversité sur la croissance des forêts. Nous avons étudié la relation diversité-stabilité dans des communautés où les populations étaient maintenues constantes, notamment en travaillant sur de courtes périodes, relativement à l'espérance de vie des arbres. Ainsi, nous avons pu étudier les mécanismes à l'origine de l'effet stabilisant de la diversité en éliminant les effets confondants liés aux dynamiques de populations (*effet de sélection* et *dynamiques compensatoires)*. L'asynchronicité de réponse aux fluctuations environnementales et les interactions entre individus, déjà connus pour leur effet stabilisant par le biais des dynamiques de populations (Tilman 1999; Hector *et al.* 2010), semblent jouer un rôle central dans la relation diversité-stabilité même en l'absence de dynamiques de populations.

Nos résultats mettent en évidence l'intérêt de considérer l'échelle individuelle dans l'étude de la relation diversité-stabilité. Par ailleurs, ils suggèrent que différents mécanismes stabilisants se produisent à différentes échelles spatiales ou temporelles et que leurs effets varient en fonction des niveaux d'organisation écologiques considérées. Enfin, nos résultats suggèrent que l'effet stabilisant de la diversité des espèces sur la productivité forestière pourrait dépendre de mécanismes affectant les niveaux trophiques supérieurs (notamment les populations d'insectes phytophages). Cette thèse s'inscrit donc pleinement dans la dynamique des études *BEF* (*Biodiversity Ecosystem Functioning*) qui vise à considérer les multiples interactions et rétroactions

entre les différents niveaux d'organisation écologiques et les différentes échelles spatiales et temporelles pour comprendre le fonctionnement des écosystèmes.

4.2.1 Mécanismes contrôlant la relation diversité-stabilité dans les écosystèmes forestiers

La Figure 4.1 synthétise les différents mécanismes stabilisants que nous avons identifiés et les relie avec d'autres mécanismes décrit dans différentes études. Nos résultats confortent l'idée que la complémentarité des espèces est à la base de la relation diversité-stabilité. Nous avons montré que la diversité pouvait stabiliser la croissance des forêts en augmentant l'asynchronicité de croissance des individus (i.e en diminuant *cov(i,j)* dans Figure 4.1). Cette asynchronicité de croissance des individus provient de la différence de leurs réponses aux fluctuations climatiques et aux insectes phytophages et dépend donc de la complémentarité des niches écologiques des espèces. Nous avons également montré que la diversité pouvait stabiliser la croissance des forêts en induisant des interactions favorables entre les individus. Ces interactions favorables peuvent augmenter la croissance individuelle (μ_i dans Figure 4.1) et réduire la réponse des arbres aux fluctuations climatiques (i.e. réduire la variance de la croissance individuelle - σ_i dans Figure 4.1). Là encore, la complémentarité des espèces est à l'origine des interactions favorables. Puisque les interactions entre individus réduisent la réponse des arbres aux fluctuations climatiques, elles pourraient également modifier les différences de réponses entre individus et donc leur asynchronicité de croissance. Toutefois, l'impact de cet effet n'a pas été évalué dans cette thèse.

En plus de son effet sur la croissance individuelle, la diversité pourrait affecter la stabilité des forêts par le biais de mécanismes se produisant à l'échelle des communautés. L'un de ces mécanismes découle de la complémentarité des espèces. Cette dernière implique une exploitation plus complète des ressources par les

communautés, ce qui pourrait augmenter leur productivité (μ dans Figure 4.1) et donc leur stabilité. La complémentarité des espèces permet, par exemple, une meilleure interception de la lumière par les communautés d'arbres, via une meilleure imbrication des houppiers. Cette utilisation plus complète de la lumière augmente la productivité des forêts (Jucker, Bouriaud & Coomes 2015; Pretzsch & Schütze 2016; Williams *et al.* 2017). Les autres mécanismes stabilisant se produisant à l'échelle des communautés dépendent des dynamiques de populations. Il s'agit de *l'effet de sélection* et des *dynamiques compensatoires*. Ces mécanismes pourraient à la fois diminuer la variance de productivité des forêts et augmenter leur productivité (Morin *et al.* 2014; Tobner *et al.* 2016).

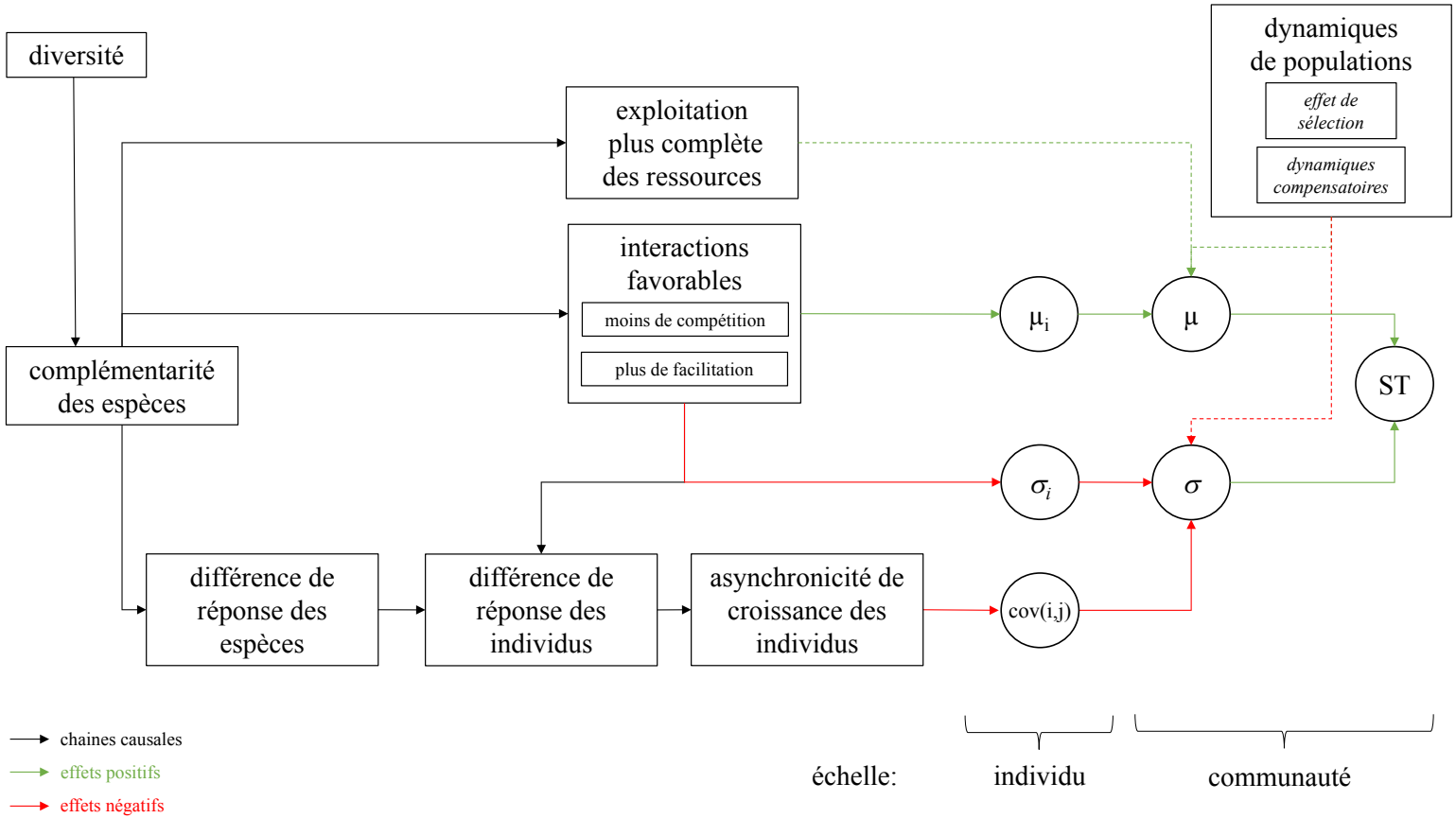

Fig. 4.1: Synthèse des mécanismes stabilisants dans les écosystèmes forestiers. Avec μ_i la croissance individuelle ; σ_i - la variance de la croissance individuelle ; *cov(i,j)* – la covariance de croissance des individus ; μ et σ la croissance à l'échelle de la communauté et sa variance, respectivement ; *ST* – la stabilité temporelle de la croissance de la communauté. Les flèches en traits pleins correspondent aux effets étudiés dans cette thèse. Les flèches en pointillés correspondent aux effets étudiés dans d'autres études.

Nos résultats suggèrent que d'autres mécanismes pourraient également moduler l'effet stabilisant de la diversité sur la productivité des forêts. La diversité pourrait, notamment, affecter la stabilité des forêts en modifiant les conditions édaphiques. Par ailleurs, nous avons observé que les interactions entre individus sont plus favorables dans les conditions édaphiques les plus stressantes, conformément à *l'hypothèse du gradient de stress* (Bertness & Callaway 1994). En modulant les interactions entre individus, les conditions édaphiques pourraient impacter l'effet stabilisant de la diversité. Nos résultats rejoignent donc les conclusions de Zhang et Zhang (2006) qui observaient, dans des communautés d'algues, un effet stabilisant de la diversité dans les milieux pauvres en nutriments mais pas dans les milieux enrichis.

4.2.2 Implications des résultats pour la gestion forestière

Nos résultats suggèrent qu'une augmentation de la diversité des espèces dans les peuplements forestiers pourrait permettre d'obtenir une productivité plus stable, notamment face aux changements climatiques et aux épidémies d'insectes, mais aussi une productivité plus élevée. Augmenter la diversité des peuplements pourrait donc être une stratégie permettant d'obtenir des revenus plus stables, et donc plus prévisibles, et plus importants. Nos résultats rejoignent ainsi un nombre grandissant d'études appelant à augmenter la diversité dans les peuplements forestiers. Des peuplements plus diversifiés pourraient, notamment, être moins sensible aux tempêtes (Schütz *et al.* 2006) ou aux invasions de pathogènes (Haas *et al.* 2011). Différents taxons, comme les oiseaux ou les plantes vasculaires, pourraient voir leur diversité augmenter avec celle des espèces d'arbres (Felton *et al.* 2010). Enfin, une augmentation de la diversité pourrait augmenter la valeur récréative des peuplements.

Afin de maximiser les effets bénéfiques de la diversité sur la productivité forestière la redondance fonctionnelle des espèces mises en mélange doit être la plus réduite possible. Autrement dit, il faut favoriser les mélanges d'espèces ayant des niches

écologiques complémentaires. Dans les zones où les épidémies d'insectes constituent un facteur important de la dynamique forestière, la priorité pourrait être donnée à des mélanges d'espèces sensibles à différents insectes phytophages. En l'absence de données précises sur l'autécologie des espèces où sur les facteurs contrôlant la croissance des forêts, une stratégie alternative pourrait consister à augmenter la diversité phylogénétique des peuplements. En effet, Paquette et al. (2015) ont montré que 50% de l'effet de la diversité fonctionnelle des espèces sur la productivité forestière pouvaient être expliquée par la diversité phylogénétique.

Si la redondance fonctionnelle peut être réduite, elle ne peut être totalement supprimée. Ainsi, même dans des communautés où cette dernière est limitée, les effets bénéfiques d'une augmentation de la diversité sur la productivité pourraient être maximaux dans les peuplements les plus pauvres en espèces. La priorité pourrait donc être donnée à la transformation des peuplements purs en peuplements mixtes. Les peuplements situés dans les conditions abiotiques les plus sévères pourraient également être prioritaires, les interactions favorables entre individus, contribuant aux effets bénéfiques de la diversité sur la productivité, y étant plus fréquentes.

4.3 Pistes de recherches futures

Cette thèse met en évidence l'effet stabilisant de la diversité des espèces sur la productivité des peuplements forestiers. Elle permet également de mieux comprendre les mécanismes qui sous-tendent la relation diversité-stabilité dans ces écosystèmes. Toutefois un certain nombre d'incertitudes demeurent.

Des études supplémentaires sont nécessaires afin de mieux comprendre comment les conditions édaphiques affectent la relation diversité-stabilité en forêt. Il s'agirait également de déterminer si l'effet stabilisant de la diversité sur la productivité forestière

et les mécanismes qui le produisent sont généralisables à tous les types de forêts dans toutes les régions du monde. Identifier la variabilité spatiale de l'effet stabilisant de la diversité pourrait permettre d'identifier des zones où une perte de diversité pourrait être plus préjudiciable qu'ailleurs. Des actions de conservation ou de restauration de la diversité pourraient être entreprises prioritairement dans ces zones.

Mesurer directement les interactions entre individus pourrait permettre de mieux comprendre leur rôle dans la relation diversité-stabilité. En effet, les interactions entre arbres sont le plus souvent estimées indirectement par des indices d'agrégation, c'est le cas dans cette thèse. Or, ces indices ont l'inconvénient d'estimer simultanément la compétition et la facilitation. Ainsi, les mécanismes biologiques ou écologiques par lesquels les interactions entre individus affectent la relation diversité-stabilité ne peuvent être identifiés. Une solution pourrait consister à mesurer la quantité de carbone échangée entre les arbres. Klein *et al.* (2016) montrent, par exemple, que 280 kg/ha/an de carbone sont échangés entre individus (conspécifiques et hétérospécifiques) dans des forêts tempérées. Comparer les échanges interspécifiques aux échanges intraspécifiques pourrait affiner notre compréhension des mécanismes à l'origine de l'effet stabilisant de la diversité.

Considérer la productivité totale des forêts (endogée + épigée) dans l'étude de la relation diversité-stabilité pourrait permettre de rapprocher les observations des attentes théoriques. En effet, les théories développées autour de la relation diversité-stabilité concernent la stabilité de la productivité totale des écosystèmes. Or, pour des raisons de simplicité, les études portant sur la productivité des forêts concernent généralement la productivité épigée. Pourtant, la productivité endogée peut représenter jusqu'à 50% de la productivité totale des forêts (Newman, Arthur & Muller 2006; Aragão *et al.* 2009). Les conclusions tirées des études faites sur la productivité épigée seule pourraient donc être biaisées. Par ailleurs, les productivités endogée et épigée semblent sensibles à des facteurs environnementaux différents. Dans les forêts

tempérées, par exemple, la productivité épigée pourrait dépendre principalement de la disponibilité en azote, tandis que la productivité endogée pourrait dépendre davantage de l'humidité du sol (Newman, Arthur & Muller 2006). Etudier la relation diversité-stabilité sur la productivité totale des forêts pourrait permettre d'identifier de nouveaux mécanismes.

Enfin, un point essentiel reste à éclaircir afin de rendre applicable les résultats obtenus dans les études portant sur la relation diversité-stabilité en forêt. Il s'agirait de déterminer si les gains en stabilité (et en productivité) obtenus par une augmentation de la diversité compensent les éventuels coûts supplémentaires liés à une gestion et à une exploitation rendue plus complexe

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